

TABLE I

Relationship between body size, time taken for defecation and gut contents in P. flava.

Number	Breadth of collar (mm)	Time taken for defecation (minutes)	Weight of gut contents (mg)
1	3	30	240.4
2	5	45	293.6
3	5	25	360.0
4	5	95	358.0
5	5	90	389.6
6	10	95	1387.8

Table I shows the relationships between the size of the animal and the time taken for the gut to empty, together with the weight of the gut contents. It may be seen that the smallest specimen takes thirty minutes, and the largest takes about ninety-five minutes to empty its gorged gut.

Another facet of ecological interest is that of the differences between the pH of the sea water and the pH of the gut content. The pH of the sea water was between 7.0 and 7.2. After blotting, a fully fed animal was held vertically by the collar region and a portion of the trunk region was cut allowing free discharge of gut contents directly onto pH papers, which indicated a pH of 9.0. From the work of Barrington (1940) it is known that the amylase contained in body extracts was active between pH 5.5 and 8.0. The significance of the high alkaline pH in the gut compared to the near neutral pH of the habitat medium is not clear. Further work is proposed.

Rate of oxygen consumption as a function of body size and maturity stage

Figure 1 (solid squares) shows the relationship between the rate of oxygen consumption of six *P. flava* during the high tide period, (see materials and methods) and body dry weight; the animals range in body weight from 89.0 mg to 325.6 mg. The rate of oxygen uptake under constant conditions was found to vary between individuals and on the basis of weight, the smallest animal consumes 0.7629 ml/g dry wt/hr, which is about one and one-half times more than that of the largest. Individual variation in the amount of oxygen consumption of an animal, for example, 89.0 mg shows a wide range of variation from 0.0191 to 0.1056 ml/hr (Table III) which may be due to the correlation between the respiratory responses and phases of the habitat tidal cycle.

A linear regression equation calculated from the observed data (Y on x) gave the following regression coefficient: $Y = -521.99x + 469.46$, where Y = the weight of the animal and x = the rate of oxygen uptake.

Data obtained on the rate of oxygen consumption of twelve specimens of *P. flava* during the late maturity stage—mature and spawning—are presented in Figure 1. Data on low tide periods and high tide periods are plotted separately. In both the periods, the rate of oxygen consumption of the smallest animal is higher than that of the largest, and the increase is about six times during the low tide period and eight times during the high tide period. The range of individual variation in oxygen uptake during the course of each experiment is wide. The

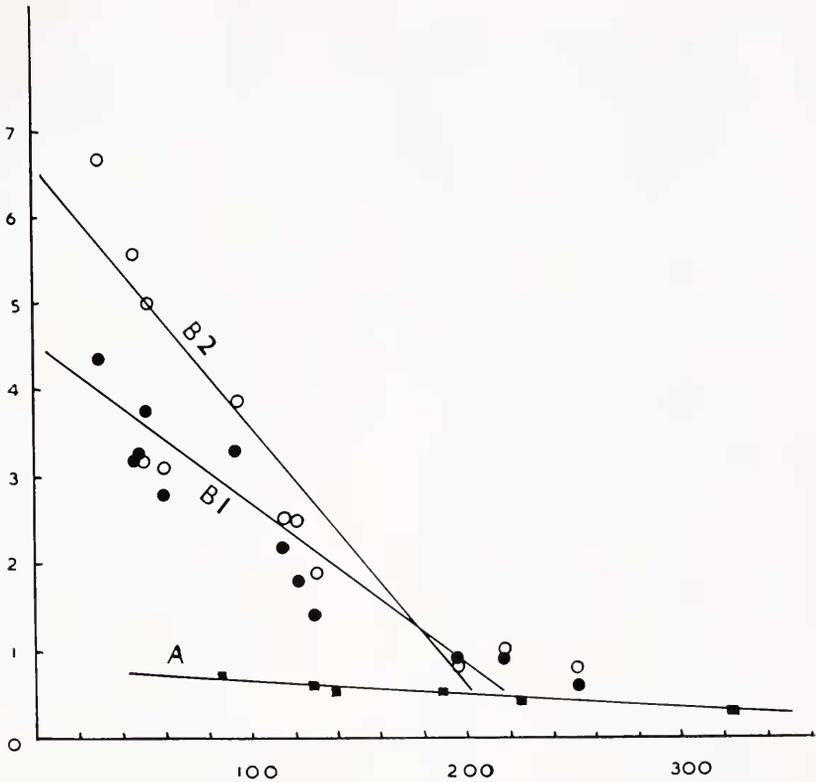


FIGURE 1. Rate of oxygen uptake of *P. flava* in relation to body weight; abscissa represents dry body weight in mg; ordinate, rate of oxygen uptake in ml/g/hr. Solid squares indicate the rate of oxygen uptake of *P. flava* during high tide periods in non-breeding season. Solid circles indicate the rate of oxygen uptake of *P. flava* during low tide periods in breeding season. Open circles indicate the rate of oxygen uptake of *P. flava* during high tide periods in breeding season. Solid lines A, B1, and B2 are the computed regression lines.

straight lines, B1 and B2, were derived statistically from low and high tide periods respectively; the regression equations being $Y = -53.63x + 244.78$ (B1) and $Y = -33.25x + 218.10$ (B2), respectively. The metabolic rate of the animals during the breeding season is higher than that of nonbreeding animals. The high tide values of the animals during both periods were subjected to Student's *t* test, and the difference between the two sets of values is statistically significant.

Oxygen uptake and tidal cycle

It is well known that periodic tidal inundations can shape behavioral and physiological responses into defined rhythms. Fluctuations in oxygen consumption over a period of time conform to tidal rhythm. Such results show three different patterns in the respiratory responses: T1, a neatly defined rhythm; T2, a tidal rhythm with additional peaks during low tides; or T3, absence of any defined rhythm correlated with phase of the tide. Data which are typical of the three

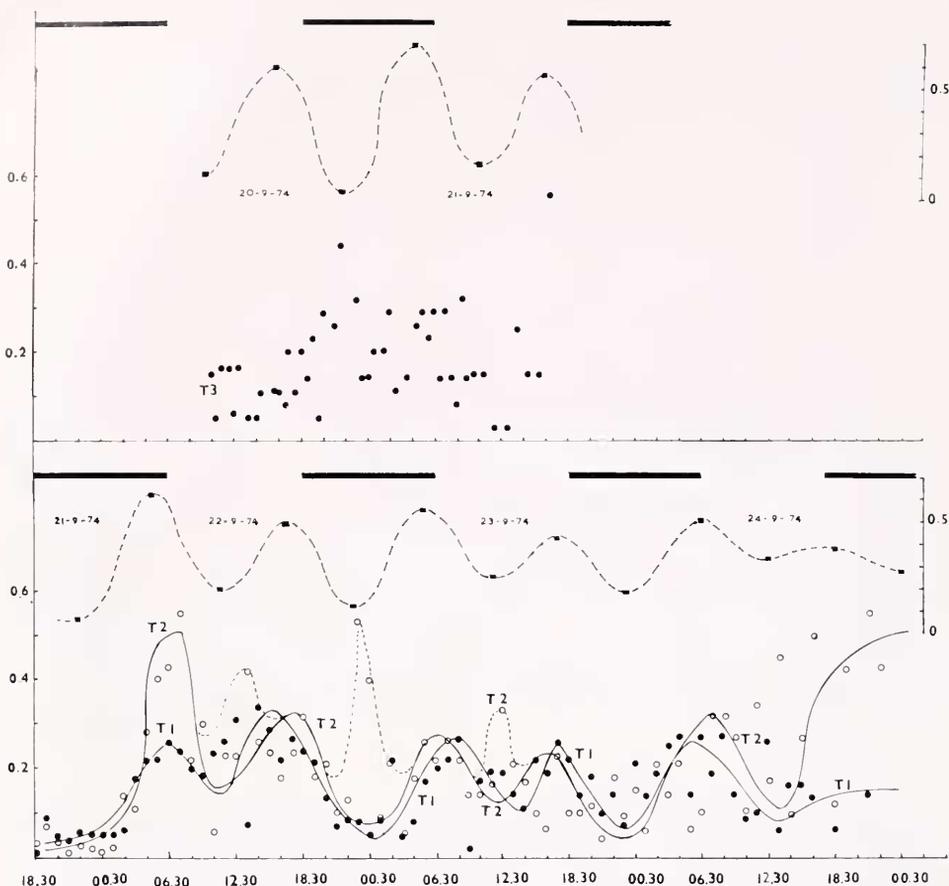


FIGURE 2. Three types of respiratory responses described in the text (T1, T2, T3) of *P. flava* to tidal cycle. The abscissae represent the times of day in hours; and the ordinates, rates of oxygen uptake in ml/hr. Solid bars represent hours of darkness in the habitat; and the ordinates in the upper right of each graph, the height of the tide in meters.

types of responses are illustrated in Figure 2, and for fifteen animals are given as the average values of oxygen uptake during the successive low and high tide periods in Table II.

Six out of fifteen specimens (T1) showed a rhythmicity in oxygen consumption whose phases seem to synchronize with some points of the habitat tidal cycle. The relationship between oxygen uptake and the tidal stages is direct, the rate of oxygen consumption being high during high tide and low during low tide.

In a further five out of the fifteen specimens (T2), besides the occurrence of a recurring rhythmicity, there was a peak value of oxygen uptake during low tide period. There remained four (T3) for which no rhythm could be detected.

Further, it is seen from Figure 2 that, when the height of the tide is lowest, the corresponding low tide values are also lowest when compared with other low

TABLE II

Data on the oxygen uptake of *Ptychodera flava* during high tide and low tide: H represents high tide period; L, low tide period; Max, maximum amount of oxygen uptake, ml/hr; Min, minimum oxygen uptake, ml/hr; OAH, average oxygen uptake during high tide periods, ml/hr; OAL, average oxygen uptake during low tide periods, ml/hr; R:LH, rate of oxygen uptake (ml/g/hr) during high tide periods; R:AL, rate of oxygen uptake (ml/g/hr) during low tide periods. Dates of experiments for the animals were: 1 to 3 on January 23-24, 1974; 4 to 7, September 20-21, 1974; 8 to 11, September 21-24, 1974; 12 to 13, September 21-22, 1974; 14 to 15, September 22-24, 1974.

Animal number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Dry weight (mg)		190.6	227.0	130.2	251.2	197.0	60.8	46.4	117.0	121.4	130.0	30.4	219.0	94.2	50.0	51.0
Tidal phase																
H		0.10012	0.10841	0.06927	0.13765	0.28213	0.18570	0.07060	0.16613	0.09120	0.04478	0.04917	0.20132	0.19478	0.23610	0.11420
L		0.07353	0.03545	0.07660	0.113693	0.11264	0.10238	0.13001	0.37298	0.31395	0.32645	0.22468	0.25004	0.37145	0.20795	0.21506
H		0.12466	0.07846	0.08880	0.23580	0.15297	0.15844	0.21783	0.35076	0.34376	0.25812	0.21616	0.23653	0.33885	0.14976	0.22236
L		0.03670	0.08183	0.18480	0.24875	0.20333	0.22037	0.44717	0.34050	0.34566	0.23988	0.26985	0.22060	0.30576	0.11895	0.29745
H		—	—	—	0.113597	0.13375	0.16650	0.27171	0.29620	0.26330	0.24137	0.10715	0.15650	0.44717	—	—
L		—	—	—	0.28337	0.17380	0.18630	0.21490	0.33000	0.26330	0.20080	0.17110	—	—	—	—
H		—	—	—	—	—	—	—	0.25543	0.14498	0.19993	0.13988	—	—	—	—
L		—	—	—	—	—	—	—	0.24520	0.20420	0.12650	0.20488	—	—	—	—
H		—	—	—	—	—	—	—	0.26518	0.21536	0.12708	0.14763	—	—	—	—
L		—	—	—	—	—	—	—	0.24900	0.32736	0.19706	0.13540	—	—	—	—
H		—	—	—	—	—	—	—	0.29376	0.22536	0.24473	0.13500	—	—	—	—
L		—	—	—	—	—	—	—	0.26076	0.39500	0.40730	0.12516	—	—	—	—
H		—	—	—	—	—	—	—	0.29974	0.30824	0.24966	0.20468	0.23532	0.36860	0.16340	0.2562
OAH		0.11289	0.09343	0.07903	0.22301	0.16325	0.18968	0.26402	0.25610	2.53000	1.92000	6.73200	1.07400	3.91200	3.26200	5.0230
R:AH*		0.58910	0.41150	0.60690	0.88770	0.82860	3.11900	5.69000	2.56100	2.53000	1.92000	6.73200	1.07400	3.91200	3.26200	5.0230
OAL		0.05511	0.05864	0.13040	0.16980	0.18960	0.17338	0.14964	0.26716	0.21947	0.18600	0.13549	0.20010	0.32693	0.16444	0.19870
R:AL*		0.28910	0.25830	1.00100	0.67590	0.96240	2.85100	3.22500	2.28300	1.80700	1.43000	4.45600	0.91360	3.47006	3.28800	3.89600
Min.		0.0205	0.01940	0.02050	0.03100	0.04880	0.07750	0.0132	0.04270	0.02440	0.00920	0.01320	0.05670	0.08710	0.03690	0.08970
Max.		0.2160	0.19220	0.13670	0.56680	0.44350	0.65010	0.4332	0.57450	0.51850	0.55370	0.34780	0.43340	0.70720	0.22950	0.49120

* Data used in Figure 1.

TABLE III

Influence of salinity on the oxygen uptake of P. flava; the change from normal sea water (30.5‰) to subnormal sea water (20.5‰) took place between 1600 and 1630 hours on January 24, 1974.

Data for the first three hours were also used in Figure 1. Mean (H) and Rate (H) refer to average oxygen uptake and rate of oxygen uptake during high tide periods.

Time	Oxygen uptake ml/hr				Summary		
	Animal 1 Dry wt 89.0 mg	Animal 2 Dry wt 140.0 mg	Animal 3 Dry wt 325.0 mg		Oxygen uptake ml/hr		
					Animal 1	Animal 2	Animal 3
13.00	—	0.0264	—	Mean (H) Rate (H) Min Max	In normal sea water (30.5‰)		
13.30	0.1056	0.1608	0.1602		0.0679	0.0811	0.1095
14.00	0.0191	0.0191	0.0370		0.7629	0.5792	0.3363
15.00	—	0.0864	—		0.0191	0.0191	0.0396
15.30	0.0571	0.1075	0.0754		0.1056	0.1608	0.1814
15.45	0.0756	0.0864	0.0935				
16.00	0.0820	—	0.1814				
16.30	0.3067	0.1142	0.0972	Mean Rate Min Max	In subnormal salinity (20.5‰)		
16.45	0.2102	0.2285	0.1085		0.1621	0.1358	0.1733
17.00	0.1401	0.1612	0.2277		0.1821	0.9700	0.5322
17.15	0.0969	0.0694	0.0874		0.0643	0.0264	0.0217
17.30	0.1180	0.2285	0.1404		0.3067	0.2285	0.3859
17.45	0.1507	0.1080	0.1099				
19.00	0.1392	0.0936	0.1837				
19.45	0.0643	0.0264	0.1814				
20.30	0.2958	0.1930	0.0630				
21.00	0.1366	0.0662	—				
22.00	0.1497	0.1242	0.0217				
22.45	0.1094	0.1613	0.2088				
00.00	0.1299	0.1005	0.3859				
1.00	0.2217	0.2261	0.2419				

tide values. The rhythm seems to be persistent for about 65 hours, and then becomes irregular or not detectable. Waning of the tidal rhythm was noticed in four animals studied for a period of 72 hours.

Salinity induced respiratory response

Data on the effect of salinity on oxygen uptake of three specimens are given in Table III. The average readings for three animals weighing 89 mg, 140 mg, and 325.6 mg in habitat sea water (30.5‰) are 0.0679, 0.0811 and 0.109 ml/hr, respectively and in reduced salinity (20.5‰) they consume 0.162, 0.136 and 0.173 ml/hr. The small specimen weighing 89.0 mg shows a difference of 0.094 ml/hr which is about 140% of the value obtained in habitat sea water; in the larger specimens, the increase being 66% (140 mg) and 58% (325.6 mg). It seems probable that the smaller animals respond more sharply than the larger animals. Response to salinity stress tends to become stabilized in a period of about an hour.

DISCUSSION

The synchronization of one or the other of the physiological processes in intertidal animals with the phase of recurring tide can result in a rhythmical temporal pattern, the tidal rhythm. A tidal rhythm of oxygen consumption seems to persist in *Ptychodera flava* under constant conditions in the laboratory. Many factors could be involved in the actual entrainment, including: locomotor activity, diurnal periodicity, tidal inundation of sea water including temperature changes, mechanical agitation, and chemical changes in the medium. In *Ptychodera flava*, since the size of the animal chamber was just big enough to house the animal, which is sluggish most of the time (Hyman, 1959), it is concluded that the periodic increase and decrease in oxygen consumption could not be attributed to the locomotor rhythms and that the peak time of oxygen consumption must be due to other factors. A circadian rhythm may persist in the absence of daily cycles of temperature or of light, with maximum consumption of oxygen during the day, and minimum during the night. Specimens of *Uca* and *Sesarma reticulatum* show both circadian and tidal rhythms (Barnwell, 1966; Palmer, 1967) in that besides coincidence of two peaks with the high water, there is a prominent nocturnal peak of locomotor activity. In *Emerita*, an exaggerated nightly activity was considered to be due to the superimposition of a diurnal rhythm on a tidal cycle (Chandrasekaran, 1965). A close observation of the results reported in the present study reveals a decline in oxygen consumption at night. Concomitant increase in oxygen consumption with high water in the early hours of the day is also evident. All of this suggests a tidal rather than a true diurnal rhythm.

This rhythm reflects the prevailing ecological conditions in the habitat. In the area enclosed by the Galaxea reef, it is significant that the lack of breaking waves and the reduction of water depth results at times in the exposure of patches of the substratum. Any corresponding variation in the activity of the animals (by deeper burrowing, for example) will involve a variation in the pattern of oxygen uptake. The pattern of oxygen consumption in five out of fifteen animals is slightly at variance with the previous pattern in that there is an increase in oxygen uptake during the low tide periods.

Laboratory observations show that *P. flava* does make nocturnal excursions on the substratum, mostly when the conditions of the habitat become unfavorable in terms of the availability of food (Azariah, unpublished). They react to environmental extremes by migrating up to the surface and lying passively. Probably, in the environment, they may be moved by the waves to other more favorable places under these conditions. Thus, the activity patterns appear more complex and influenced by more than one factor.

Four animals did not show any tidal rhythm. The observations were made on the four animals simultaneously, and hence their pattern is a reflection of the pattern of the tidal cycle prevailing during the time of those particular experiments. The absence of tidal rhythm may result from the necessity for "conditioning" the animal to the experimental set-up used. In data obtained towards the end of the experiments (after about 20 hours), the animals show a tendency to exhibit a rhythm.

Enright (1963) reported that the activity levels of the amphipod *Synchelidum* were related to the amplitude of the tides. The activity rhythm of the sand crab *Emerita asiatica* coincided with the amplitude of the tide (Chandrasekaran, 1965). A similar relationship in *P. flava*, together with the waning of the tidal rhythms with time, suggests that the rhythm is phased by the environmental variables.

It is interesting to note the relationship between salinity changes and metabolism of *P. flava*. It responds to subnormal salinity by an increase in the respiratory rate, agreeing with the reports of Schlieper (1929), and Potts and Parry (1964). Although the increased respiration may suggest a causal relation to requirements for osmotic work, Potts and Parry (1964) and Vernberg and Vernberg (1972) suggest that changes in salinity may alter the locomotor activity of an organism, and hence changes in metabolic rate may reflect behavioral changes rather than the effect of salinity on basic metabolic processes (see Duncan, 1966). In *P. flava* no attempt was made to study its behavioral response to salinity changes. The pronounced rise in the respiratory rate on sudden changes of salinity and its gradual decline followed by the maintenance of a higher level of oxygen consumption than that of the one prior to exposure to a new salinity regime, show its short term overshoot reaction and the longer continuing responses. There seems to be a conflict between the inherent tidal rhythm and salinity-induced changes in respiration; there is a tendency to keep to the rhythm of tide, but the influence of salinity changes is dominant.

Time at Krusadi Island was limited, data were processed at Madras, and further experiments were impossible. Further work, following the suggestions given by Kinne (1971), is now planned.

We thank Dr. K. Ramalingam, Professor, Department of Zoology, University of Madras, Madras-600005 and Professor H. Mohamed Mohideen, Principal, New College, Madras-600014 for their interest and encouragements. Our thanks are due to the members of the staff at the Central Marine Fisheries Research Institute, Mandapam Camp and State Fisheries (Marine Biology) for their kind co-operation. One of us (J. A.) wishes to thank the University of Madras for financial assistance. We thank Prof. C. L. Herreid, Department of Biology, State University of New York at Buffalo, for useful discussion and help in statistical analyses.

SUMMARY

1. Some aspects of the ecology and respiratory physiology of *Ptychodera flava* have been studied.

2. Increase in body weight involves a decrease in the rate of oxygen consumption. At high tides, the rates of oxygen uptake of nonbreeding *P. flava* are 0.7629 (smallest) and 0.3363 (largest) in ml/g/hr. At high tides, mature and spawning female rates are 6.732 (smallest) and 0.8877 (largest) ml/g/hr. Rate of oxygen uptake is a function both of body size and of maturity stage in *P. flava*.

3. Respiratory responses of 15 specimens of *P. flava* fell into three classes: 1, showing a rhythm synchronized with tidal phases; 2, showing a tidal rhythm with additional peaks during low tides; or 3, with no detectable rhythm.

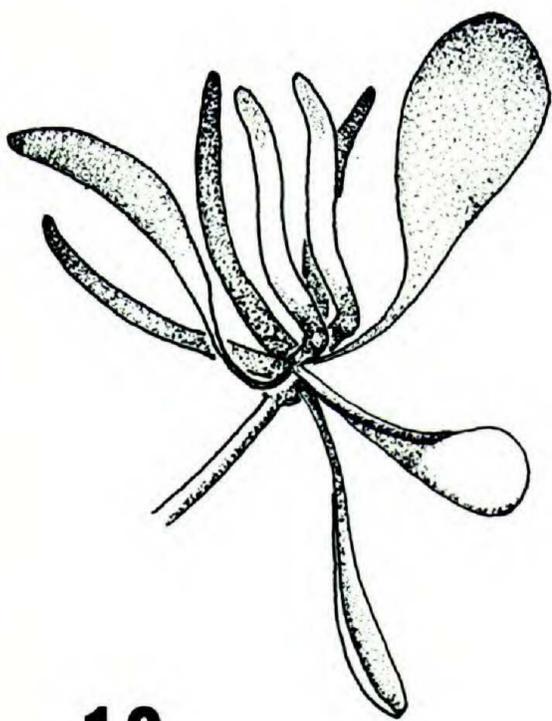
4. *P. flava* reacts to lowered salinity by showing a sudden rise in respiration. The sustained level of respiration is subsequently a little higher than in normal sea water.

5. The deep-seated tidal rhythm shows variations, and it is suggested that locomotor activity, spawning, temperature, and salinity may all be factors involved.

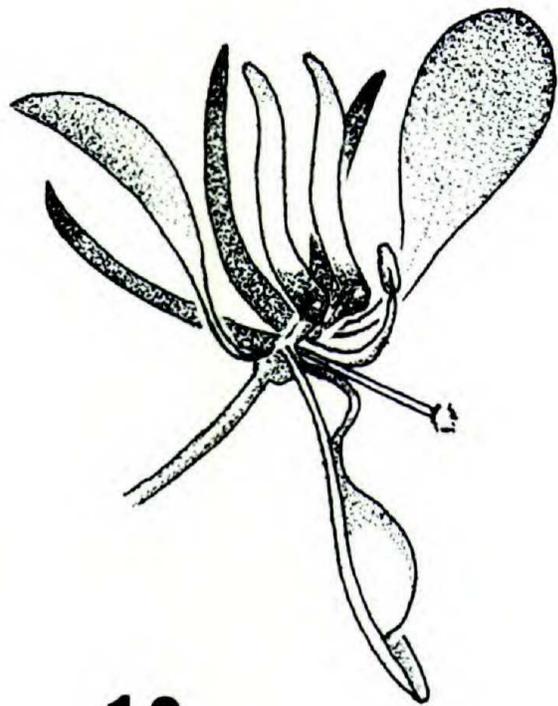
LITERATURE CITED

- ASHWORTH, R. B., AND M. J. CORMIER, 1967. Isolation of 2,6-dibromophenol from the marine hemichordate, *Balanoglossus biminienis*. *Science*, **155**: 1558-1559.
- AZARIAH, J., 1969. Physiological and histochemical studies on some protochordates. *Ph.D. thesis, University of Madras, India*, 105 pp.
- BARNWELL, F. H., 1966. Daily and tidal patterns of activity in individual fiddler crabs (Genus *Uca*) from the Woods Hole region. *Biol. Bull.*, **130**: 1-7.
- BARRINGTON, E. J. W., 1940. Observations on feeding and digestion in *Glossobalanus minutus*. *Quart. J. Microscop. Sci.*, **82**: 227-260.
- BARRINGTON, E. J. W., 1965. *The Biology of Hemichordata and Protochordata*. Oliver & Boyd, London, 176 pp.
- CIANDRASEKARAN, M. K., 1965. Persistent tidal and diurnal rhythms of locomotory activity and oxygen consumption in *Emerita asiatica* (M. Edw.) *Z. Vergl. Physiol.* **50**: 137-150.
- DE JORGE, F. B., AND J. A. PETERSEN, 1968a. Accumulation of "glycogens" in the genital region of *Balanoglossus gigas* Fr. Muller (Spengel, 1893) Enteropneusta during reproduction. *Comp. Biochem. Physiol.*, **26**: 737-740.
- DE JORGE, F. B., AND J. A. PETERSEN, 1968b. Comparative biochemical studies on *Balanoglossus clavigerus* and *Willeyia loya* (Enteropneusta). *Comp. Biochem. Physiol.*, **27**: 551-557.
- DE JORGE, F. B., J. A. PETERSEN, AND P. SAWAYA, 1967. Biochemical studies on the enteropneust *Balanoglossus gigas* (Fr. Muller, 1898). *Comp. Biochem. Physiol.*, **22**: 467-475.
- DEVANESAN, D. W., AND P. I. CHACKO, 1942. *Balanoglossus* as food of fishes. *Curr. Sci.*, **11**: 242-243.
- DUNCAN, A., 1966. The oxygen consumption of *Potomopyrgus jenkinsi* (Smith) (Prosolvanchiata) in different temperatures and salinities. *Verh. Int. Ver. Limnol.*, **16**: 1739-1751.
- ENRIGHT, J. T., 1963. The tidal rhythm of activity of a sand-beach amphipod. *Z. Vergl. Physiol.*, **46**: 276-313.
- FRY, F. E. J., AND J. S. HART, 1948. The relation of temperature to oxygen consumption in the gold fish. *Biol. Bull.*, **94**: 66-77.
- HYMAN, L. H., 1959. *The Invertebrates*, Volume 5. McGraw-Hill Book Company, Inc., New York, 783 pp.
- JAYARAMAN, N., 1954. Seasonal variations in salinity, dissolved oxygen and nutrient salts in the inshore waters of the Gulf of Mannar and Palk Bay near Maudapam (S. India). *Indian J. Fish.*, **1**: 345-364.
- JOB, S. V., 1955. The oxygen consumption of *Salvelinus fontinalis*. *University of Toronto Biological Series*, **61**: 1-39.
- KINNE, O., 1971. Salinity animals, invertebrates. Pages 821-995 in O. Kinne, Ed., *Marine Ecology*, Volume 1, Part 2. Wiley-Interscience, John Wiley & Sons Ltd., London.
- KRISHNAN, G., AND P. GOVINDARAJULU, 1968. Observations on the biochemical composition of the enteropneust *Ptychodera flava*. *Life Sci.*, **7**: 629-632.
- KURIYAN, G. K., 1949. On the occurrence of Enteropneusta in Shingle Island, Gulf of Mannar. *Curr. Sci.*, **18**: 258.
- MACHA, N., 1969. A histochemical study of epidermal mucous secretion in Enteropneusta. *Acta Histochem.*, **34**: 305-309.
- MUTHU, M. S., 1956. Studies on Plankton. *M.Sc. thesis, University of Madras, Madras, India*.
- PALMER, J. D., 1967. Daily and tidal components in the persistent rhythmic activity of the crab, *Scorpaena*. *Nature*, **215**: 64-66.

- PETERSEN, J. A. AND L. LONGHI, 1971. Amino acid distribution in *Glossobalanus* (Ptychoderoidea, Enteropneusta Hemichordata). *Histochemistry*, **16**: 323-327.
- POTTS, W. T. W. AND G. PARRY, 1964. *Osmotic and ionic regulation in animals*. Pergamon Press, London, 423 pp.
- RAMANUJAM, S. G. M., 1935. Enteropneusta from Krusadi Island. *Curr. Sci.*, **3**: 427.
- RAO, K. P., 1954a. The early development of Enteropneusta *Ptychodera flava* Eschscholtz. *J. Zool. Soc. India*, **6**: 145-152.
- RAO, K. P., 1954b. Bionomics of *Ptychodera flava*. *J. Madras Univ.*, **24B**: 1-5.
- RAO, K. P., 1955a. Enteropneusta from Madras and the Gulf of Mannar, with a note of the probable course of distribution of *P. flava* Eschscholtz. *Proc. Indian Sci. Congr.*, **44**: 301.
- RAO, K. P., 1955b. Morphogenesis during regeneration in an Enteropneust. *J. Anim. Morphol. Physiol.*, **1**: 1-7.
- SCHLIEPER, C., 1929. Über die Einwirkung niedriger Salzkonzentrationen auf marine Organismen. *Z. Verg. Physiol.*, **9**: 478-514.
- SUNDARA RAO, P. J., AND S. RANGA RAO, 1949. A note on the occurrence of a giant Balanoglossid at Krusadi Island. *J. Bombay Natur. Hist. Soc.*, **48**: 813.
- UDAYAVARMA, T. P. AND C. V. GANGADHARA REDDY, 1959. Seasonal variations of the hydrological factors of the Madras coastal waters. *Indian J. Fish.*, **6**: 298-305.
- VERNBERG, W. B. AND F. J. VERNBERG, 1972. *Environmental physiology of marine animals*. Springer-Verlag, Berlin, 346 pp.



12



13

FIGURES 12-13. Flowers of *Lopezia racemosa*, 5.—12. Before snapping of fertile stamen upward; it is held in place and under tension by enfolding staminode.—13. After fertile stamen has snapped upward and staminode moved downward; the style has grown outward and the stigma occupies essentially the position of the fertile anther in Fig. 12.

that the shedding anther did previously (Fig. 13). Outcrossing species of *Lopezia* are thus strongly protandrous, and a pollinator moving from flower to flower has a high probability of effecting cross-pollination.

This general outline of floral biology holds for the bird-pollinated species of *Lopezia* (*L. semeiandra*, *L. longiflora*, *L. grandiflora*, *L. langmaniae*). In all species of sect. *Lopezia*⁵ the rotated fertile anther is held under tension by the enfolding staminode and snaps the pollen up onto the venter of any fly that alights and orients itself toward the pseudonectaries. This interesting phenomenon has been observed and discussed by many students for nearly 200 years (reviews in Raven *et al.*, 1974; Eyde & Morgan, 1973). The snapping phenomenon is not found in the four species of sect. *Pelozia*, nor in the autogamous *L. gracilis* (sect. *Nannolopezia*).

Because of the distribution of the snapping phenomenon among the species of *Lopezia*, we hypothesize that it evolved in the common ancestor of sect. *Lopezia*, and that the evolution of the mechanism was a single, unique event. This implies that sect. *Pelozia* was derived from its common ancestor with sect. *Lopezia* before the evolution of the snapping mechanism. It also lends support to the notion that *Lopezia gracilis*, the only species of sect. *Nannolopezia*, was not derived from sect. *Lopezia*, contrary to Fig. 11.

Morphological variation in the staminode is fairly extensive and useful in some instances in evaluating the degree of similarity between taxa. It is variable in length, proportion, and outline, as well as in color. In *Lopezia laciniata* and *L. gentryi*, not characterized by the snapping mechanism, it is linear and concave;

⁵ Unfortunately, we have not been able to examine one of the most critical species assigned to this group, *L. hintonii*, in a living condition.

in the autogamous *L. riesenbachia* and *L. clavata*, it is broad and indistinctly clawed; and in most fly-pollinated species, it is somewhat spoon-shaped and very distinctly clawed, the blade enfolding the fertile stamen and holding it under tension at maturity. A reduced uniloculate anther has been observed very rarely on the staminode in *L. grandiflora* and in *L. langmaniae*.

Capsules.—The main morphological characters of the capsule are size and shape. The largest capsules are found in *Lopezia lopezioides*, *L. grandiflora*, *L. trichota*, whereas *L. gracilis* and *L. gentryi* have the smallest ones. Slight differences in size, however, have been observed between the members of related pairs of species such as *L. miniata* and *L. racemosa*, *L. nuevo-leonis* and *L. miniata*, *L. clavata* and *L. sinaloensis*. Several species are distinguished by the shape of their fruits: *L. clavata*, *L. sinaloensis*, *L. riesenbachia* with \pm cylindrical capsules; *L. nuevo-leonis* with oblong-ellipsoid capsules; *L. cornuta* with angularly oblong-obovoid and horned at apex capsules; *L. gentryi* with setose-tubercled capsules and *L. laciniata* with obovoid-obconical ones. Most of the others have subglobose capsules.

The seeds of *Lopezia* are ballistically dispersed from the wind-shaken, open capsules. A few seeds remain at the bottom, and they just fall with or from the dry capsule. The seeds of *L. lopezioides* are narrowly winged, as if they might be adapted to anemochory, but they are so heavy and their wings so narrow that this scarcely seems possible.

In a few species such as *Lopezia trichota* and *L. semeiandra* the capsules have thick valves which sometimes dehisce tardily or do not open at all while still on the plant. In these cases the capsule is the dispersal unit and is presumably dispersed by streams.

Seeds.—Species of *Lopezia* are often distinguished sharply by the texture of their seeds. In *L. grandiflora*, *L. longiflora*, and *L. langmaniae* the seeds are coarsely long-tubercled; in *L. trichota*, *L. smithii*, *L. cornuta*, and *L. nuevo-leonis* they are also coarsely tubercled but with rounded tubercles; the seeds of other species are \pm finely tubercled. The tubercles or papillae are transversely arranged in *L. conjugens*, *L. riesenbachia*, and *L. sinaloensis*, \pm so in *L. racemosa* subsp. *moelchenensis* and *L. nuevo-leonis*; they are longitudinal in *L. gracilis* and *L. semeiandra*. The seeds of *L. trichota* are transversely wrinkled and also somewhat marginate; in *L. lopezioides* the seeds are smooth and distinctly winged. *Lopezia lopezioides* also has the largest seeds in the tribe. Relatively large seeds occur in *L. longiflora* and *L. cornuta*; relatively small seeds are found in *L. miniata*, *L. ciliatula*, *L. riesenbachia*, *L. clavata*, and *L. laciniata*. No significant differences in shape have been observed.

Chromosome numbers.—When known, these are given in the present paper. Documentation for the chromosome numbers cited here will be given by Plitmann, Tai, and Raven (1974). Results of experimental hybridizations will likewise be reported in due course.

RELATIONSHIPS OF THE TRIBE

One of the six tribes of Onagraceae (Raven, 1964), Lopezieae are sharply set off from all others by their 4-merous flowers and 2-merous androecium. Although the chromosomes of Lopezieae are unspecialized (Kurabayashi, Lewis & Raven, 1962) and some species retain the original basic chromosome number for the family Onagraceae, $n = 11$, Lopezieae do not appear closely related to Fuchsieae and even less so to Circaeae, the other two tribes that have a similar chromosomal constitution. The traditional grouping of Lopezieae with Circaeae (*e.g.* by DeCandolle, 1828; Spach, 1835; Baillon, 1877; and Raimann, 1893) seems to have to do with nothing more than their common possession of two stamens (Eyde & Morgan, 1973). Recently Eyde and Morgan (1973) have postulated a connection between Jussiaeae and Lopezieae on the basis of their similar nectaries, unique in the family, and lack of a floral tube. Further studies of additional characteristics will help to elucidate these reticulate relationships, but their nature leads one to emphasize the rather isolated position of the tribe Lopezieae within the family.

GENERIC LIMITS

It has been traditional to recognize four genera—*Diplandra*, *Lopezia*, *Riesenschbachia*, and *Semeiandra*—in the tribe Lopezieae (Endlicher, 1840, 1841; Bentham & Hooker, 1862; Raimann, 1893). In 1877, Baillon placed *Riesenschbachia* and *Semeiandra* in the synonymy of *Lopezia*, retaining *Diplandra* as distinct. Although T. S. Brandege (1889: 158) wrote in favor of such a generic alignment, apparently it has not been followed by other authors. In 1909, Rose described three additional ones: *Pelozia*, *Jehlia*, and *Pseudolopezia*. He segregated them from *Lopezia* largely on the basis of petal morphology and the degree of adnation and connation in the flower. In the most recent overall revision, Munz (1961) recognized *Diplandra*, *Lopezia*, *Riesenschbachia*, *Semeiandra*, and *Pseudolopezia*, but not *Jehlia* or *Pelozia*. He frankly admitted that his decisions about the limits of genera were arbitrary, and that the matter needed further study. The next year Miranda (1962) reemphasized the distinctiveness of *Lopezia langmaniae* (Miranda, 1953) and argued for the recognition of *Jehlia*. Thus the question of generic alignments in Lopezieae has been a vexed one, with nearly every student of the group having a different opinion.

Our studies and particularly those of Eyde and Morgan (1973) have shed new light upon relationships within Lopezieae; Eyde and Morgan's findings are summarized in Fig. 11 (reprinted from Eyde and Morgan, 1973: 123). A table of the sections and species we recognize was given on p. 479. The most distinctive units within the tribe are *Lopezia lopezioides* (sect. *Diplandra*) and *L. semeiandra*-*L. riesenschbachia* (sect. *Riesenschbachia*; the genera *Semeiandra* and *Riesenschbachia*). *Lopezia lopezioides* is the only member of the group that retains two fertile stamens; yet its flowers are highly zygomorphic, its ovules have been reduced to one per locule, and its stilar bundles are relatively indistinct. Its subopposite leaves may or may not be primitive, and it shares the original basic chromosome number of the group, $n = 11$, with several other species. On the other hand, *L. longiflora* (the section or genus *Pseudolopezia*), although it has only one fertile

stamen, has the most radially symmetrical flowers in the group, ones that might in all respects other than their androecial condition be considered most generalized. *Lopezia semeiandra* (the genus *Semeiandra*) and *L. riesenbachia* (the genus *Riesenbachia*) have virtually identical floral tubes, so much so that they must be considered to have had a common ancestor with a tube of this sort and the chromosome number which they share in common, $n = 9$. Despite this communality of features, the contrast between the large, red, hummingbird-pollinated flowers of *L. semeiandra* and the small, purplish, autogamous ones of *L. riesenbachia* is, as Eyde and Morgan (1973) have pointed out, rather startling. Their capsules and seeds differ markedly, and they occur in very different situations ecologically.

In view of these highly reticulate relationships, it seems to us that there is nothing to be gained by removing up to five monotypic genera (*Diplandra*, *Jehlia*, *Pseudolopezia*, *Riesenbachia*, and *Semeiandra*) from a small genus of 21 closely related species. *Pelozia* has been recognized as distinct only by its author (Rose, 1909) and by Sprague and Riley (1924), Riley (1924), and Willis (1966); other authors have followed the lead of M. E. Jones (1929) and declined to regard it as generically distinct. Floral evolution has evidently been rapid in this group, and adaptation to different pollination systems has resulted in the production of a number of superficially very different but fundamentally similar floral types within the group. We wish to emphasize the unity which binds together these species is a whole array of geographical, morphological, anatomical, and cytological features, and believe that to group them in a single genus is the preferable way of expressing the pattern of diversity in the tribe. Suggestions that *Lopezieae* may be polyphyletic (Baehni & Bonner, 1948) are certainly without merit, in the light of recent research. Less diversity characterizes the resulting group than is found in *Ludwigia*, *Camissonia*, *Oenothera*, *Fuchsia*, or even the ditypic *Gongylocarpus* as currently recognized. In *Lopezia*, there is an impression of greater diversity owing to the spectacular changes that have occurred in floral conformation in relation to specific pollination systems, enhanced by early trends toward zygomorphy in the group. Nevertheless, the overall impression is of a group of relatively closely related species in which an impressive degree of adaptive radiation, affecting mostly the flowers, has taken place.

THE DELIMITATION OF SECTIONS IN *LOPEZIA*

Earlier efforts to subdivide *Lopezia* have not been extensive, although Sprague and Riley (1924) recognized two groups—Unituberculatae and Bituberculatae—depending upon the number of glands on the upper petals. Most other authors have tacitly assumed that the six segregate genera deserved formal recognition when included within *Lopezia*, but few such groups have actually been given names.

It follows from the discussion given above and by Eyde and Morgan (1973) that *Lopezia lopezioides* (*Diplandra*); *L. semeiandra* and *L. riesenbachia* (*Riesenbachia*); and the group earlier segregated as *Pelozia* (including *L. clavata*, *L. sinaloensis*, *L. laciniata*, and *L. gentryi*) deserve recognition as distinct sections

within the genus. We have chosen to emphasize the extensive similarities in floral anatomy between *L. semeiandra* and *L. riesenbachia* by combining them within a single section, even though their differences in external morphology, pollination system, and ecology are great.

Most of the remaining species are relatively closely related, and it would be defensible to group them within a single variable section. Nevertheless, it appears reasonable to segregate as sect. *Jehlia* (including *Pseudolopezia*) the three species characterized by bird pollination, tubular red flowers, and a chromosome number $x = 11$, from the remainder, which are fly-pollinated or autogamous, have more strongly zygomorphic, rose-purplish, lavender, or white flowers in which the petals and sepals spread at right angles from the top of the ovary, and chromosome numbers of $n = 10$ (or 20), 9, 8, or 7.

Among the remaining 12 species of *Lopezia*, *L. gracilis* stands out in floral anatomy and morphology (Eyde & Morgan, 1973). It is highly autogamous, and shares with the distantly related *L. gentryi* the lowest gametic chromosome number in the genus, $n = 7$. Unlike the other 11 species, which are probably closely related and derived from a single common ancestor, *L. gracilis* does not exhibit the snapping phenomenon, and there is no reason to consider it derived from ancestors that did exhibit this mechanism for outcrossing. Similar reasoning applies to the four species of sect. *Pelozia*, in which the union of floral parts is much more advanced than in *L. gracilis*. We believe that the relationships of the latter species are best indicated by segregating it as a monotypic section, coordinate with sect. *Pelozia* and sect. *Lopezia* and with them representing the greatest degree of floral specialization in the genus.

In setting up these six sections within the genus *Lopezia*, we have attempted to follow the reasonable standards established for the genus *Clarkia* by Lewis and Lewis (1955). Each section consists of one or more demonstrably closely related species between which hybridization may be possible. We have not yet succeeded in obtaining intersectional hybrids within the genus *Lopezia*.

GEOGRAPHY, ECOLOGY, AND PHYLOGENY

A majority of the 25 taxa of *Lopezia* recognized in the present revision occur in the following four regions:

I. West slope of the Sierra Madre Occidental, south to its junction with the Trans-Mexican Volcanic Belt in Colima. Thirteen taxa occur in this area, of which ten are restricted to it.

II. Sierra Madre along the Pacific Coast from Colima to the Isthmus of Tehuantepec. Nine taxa, five endemic.

III. Nuclear Central America, principally Chiapas and Guatemala. Four taxa, two endemic.

IV. Sierra Madre Oriental and western slopes of the Chihuahuan Desert. Four taxa, two endemic.

Two taxa occur beyond the limits of these four regions. They are *Lopezia miniata* subsp. *paniculata*, restricted to El Salvador, Costa Rica, and Panama; and *L. clavata*, found in southern Baja California. Only four taxa occur in more

than one region: *L. miniata* subsp. *miniata*, *L. racemosa* subsp. *racemosa*, *L. semeiandra*, and *L. grandiflora* subsp. *macrophylla*.

Although species of *Lopezia* are distributed widely in almost all of the mountainous areas of Mexico from northern Sonora in the west and central Nuevo León in the east southward to the Isthmus of Tehuantepec, it seems clear that their chief region of diversification and evolution has been the mountainous areas along the Pacific Coast. The Sierra Madre Occidental and the coastal ranges south to Oaxaca have been elevated since the late Cretaceous, perhaps 70 million years ago (Schuchert, 1935; Malfait & Dinkelman, 1972), whereas much of the remainder of Mexico was under the sea until much more recently. There is no concrete evidence for the evolution of the Onagraceae before the Paleocene, perhaps 65 million years ago (Krutzsch, 1968; Muller, 1970; Eyde & Morgan, 1973). As bird pollination can be shown convincingly to be the primitive system in *Lopezia* (Eyde & Morgan, 1973), and in view of the doubtful existence of specialized flower-visiting birds before Neogene time (J. Cracraft, personal communication), it would be difficult to imagine the existence of *Lopezia* or its immediate ancestors before the start of the Miocene, perhaps 25 million years ago, if that early. By this time, there was ample scope for radiation in relation to the diverse habitats of the Sierra Madre Occidental and coastal ranges to the south, and a variety of mesic and temperate habitats in which to survive temporarily unfavorable climatic episodes.

One can assume with confidence that the spread of *Lopezia* south of the Isthmus of Tehuantepec was an event of the upper Tertiary or Pleistocene, and that the evolution of *L. miniata* subsp. *paniculata* (from *L. miniata* subsp. *miniata*) and *L. langmaniae* (from *L. grandiflora*-like ancestors) were events of the past few million years. Two species of the genus, *L. miniata* and *L. racemosa*, are extremely widespread and weedy; they have probably spread to occupy much of the total range of the genus only in the upper Pleistocene and more recently, in part because of the spread of swidden agriculture four to six thousand years ago.

Reviewing now the ecology of *Lopezia* in broad terms, we offer the following summary by habitat type:

I. Dry understory of pine-oak forests: *Lopezia grandiflora*, *L. hintonii*, *L. longiflora*, *L. lopezioides*, and *L. smithii*. It may be that *L. racemosa* and *L. miniata* are principally associated with this habitat, but they have now spread widely into other disturbed habitats at middle elevations.

II. Moist seeps and streambanks in pine-oak forest: *Lopezia cornuta*, *L. gentryi*, *L. gracilis*, and *L. laciniata*.

III. Grassland (páramo) and other open places in cloud forest: *Lopezia miniata* subsp. *paniculata*.

IV. Tropical deciduous forest, especially along ravines and in other protected places: *Lopezia ciliatula*, *L. clavata* (nearly to sea level), *L. conjugens*, *L. langmaniae*, *L. riesenbachia* (to sea level), *L. semeiandra*, *L. sinaloensis*, and *L. suffrutescens*.

V. Stony ravines in piñon-juniper woodland: *Lopezia trichota*.

Comparing this summary with Fig. 11 (from Eyde & Morgan, 1973), it becomes abundantly clear that the principal site of evolution of *Lopezia* has been the pine-oak forest of the Sierra Madre Occidental and Pacific Ranges southward in Mexico. Much of the evolution of species within the genus has been in relation to the exploitation of relatively xeric habitats along the margins of the range of the group. Many of the species occur in pine-oak forest at middle elevations. A number of the species found in the Sierra Madre Occidental and other Pacific Coast ranges are restricted to one or two localities, not more than 150 km apart. These include: *Lopezia ciliatula*, *L. conjugens*, *L. grandiflora* subsp. *grandiflora*, *L. hintonii*, *L. laciniata* subsp. *ovata*, *L. longiflora*, *L. sinaloensis*, *L. smithii*, and *L. suffrutescens*. Other taxa have somewhat wider ranges in this region—the widest is *L. semeiandra*, which extends for more than 700 km in the interface between the Tropical Deciduous Forest and the pine-oak woodlands from northern Sinaloa to the northern edges of the Río Balsas drainage in southern Michoacán—but the overall picture is one of local endemism, rapid evolution, and especially survival of unusual taxa on a very local basis.

Most species of *Lopezia* flower in the first half of the dry season (October to December), and many continue for two or three months beyond this time. The widespread, weedy, polymorphic *L. racemosa* often flowers in the latter half of the rainy season (August, September). It is thus modally distinct from the equally widespread and weedy *L. miniata*, with which it can be hybridized. In general, the species most characteristic of xeric habitats, such as *L. trichota*, *L. clavata*, and *L. sinaloensis*, flower toward the end of the rainy season. *Lopezia gracilis*, which grows at relatively high elevations toward the northern end of the range of the genus, likewise flowers at the end of the period of summer rainfall.

In general, the pattern of evolution in *Lopezia* seems to have involved the derivation of ecologically or geographically marginal species which are relatively uniform morphologically from more widespread, variable ones. From polytypic and relatively widespread species such as the present-day *Lopezia grandiflora*, *L. miniata* subsp. *miniata*, *L. racemosa* subsp. *racemosa*, and *L. laciniata* have been derived such relatively uniform ones as *L. langmaniae*; *L. miniata* subsp. *paniculata*, *L. cornuta*, and *L. ciliatula*; *L. racemosa* subsp. *moelchenensis* and *L. conjugens*; and *L. gentryi*. As will be detailed in the paragraphs that follow, and discussed further in the systematic portion of this paper, such changes have often been accompanied by aneuploid changes in chromosome number and also by increased autogamy. Such evolutionary patterns are common in flowering plants, and it has been pointed out for example by Fisher (1965) that species of a given group found on "unusual" substrates are often much less variable morphologically than their widespread relatives.

The evolution of *Lopezia nuevo-leonis* ($n = 8$) appears to have taken place in locally favorable habitats on the dry slopes of the Sierra Madre Oriental from ancestors similar to *L. miniata* ($n = 10$). Similar aneuploid changes in chromosome number in relation to the occupation of marginal habitats by annual taxa appear to have taken place in the evolution of *L. ciliatula* ($n = 9$) from *L. miniata* ($n = 10$) and of *L. gentryi* ($n = 8, 7$) from *L. laciniata* subsp. *ovata*

($n = 10$), as well as in the presumably earlier evolution of *L. gracilis* ($n = 7$) and *L. clavata* ($n = 9$) from unknown ancestors with higher chromosome numbers, probably $n = 10$. These changes are reminiscent of those so elegantly documented by Lewis and his colleagues (*e.g.* Lewis & Lewis, 1955; Lewis & Roberts, 1956; Lewis, 1962, 1973) for *Clarkia*, an unrelated annual genus of Onagraceae, tribe Onagreae, and found also in other groups of annual plants (Stebbins, 1950). They may also be analogous with those that were involved in the evolution of plants with $n = 10$ (ancestors of sect. *Lopezia*) from those with $n = 11$, early in the history of the genus; the evolution of $n = 9$ in *L. suffrutescens*, presumably from ancestors with $n = 10$; and the evolution of other plants with $n = 9$ (common ancestor of *L. semeiandra* and *L. riesenbachia*), thought to have been an evolutionary event of some antiquity.

Lopezia trichota is the most divergent species of sect. *Lopezia* in terms of its pattern of ecological adaptation. Its underground parts are extremely swollen and bulbous, and its annual stems wither completely early in the dry season. Its tardily dehiscent capsules seem to be spread along streams and by periodic flooding. This species, which was presumably derived from ancestors somewhat similar to *L. racemosa*, occurs on dry slopes on both sides of the Chihuahuan Desert.

The stoloniferous habit of *Lopezia laciniata* (sect. *Pelozia*) is an obvious adaptation to the moist, mossy seepages on the faces of cliffs that it inhabits. A similar habit—that of rooting at the nodes from decumbent branches—is also characteristic of *L. racemosa* subsp. *moelchenensis* (sect. *Lopezia*), which occurs on somewhat protected limestone cliffs in Chiapas and Guatemala. Like a few populations of *L. racemosa* subsp. *racemosa*, *L. racemosa* subsp. *moelchenensis* is polyploid, with $n = 20$. The only other consistently polyploid taxon in *Lopezia* is *L. longiflora*, with $n = 22$; its ancestors are unknown and presumably extinct.

Also deserving special comment is the species pair *Lopezia clavata* (southern Baja California) and *L. sinaloensis* (Sinaloa). The former is an autogamous annual that occurs in colonies in the arroyos and on protected slopes. Its flowers are quite variable, as might be expected in a colonial, autogamous species that presumably is rarely visited by insects. Unfortunately, its mainland relative, *L. sinaloensis*, is known only from the type collection. Until it can be rediscovered, it will be difficult to evaluate precisely the relationship between the two, a matter of considerable interest.

To summarize the pattern of evolution within *Lopezia*, the group seems to have originated during or shortly before the Miocene in the pine-oak forest of the Sierra Madre Occidental of Mexico. The derivation of fly-pollinated and autogamous species from bird-pollinated ancestors and the occupation of increasingly xeric habitats, as well as secondary ones, with the development of annual taxa, appear to have been major trends that occurred subsequently. Connation and adnation among floral parts and the development of increasingly zygomorphic flowers are among the morphological and anatomical trends that accompanied the phylogenetic elaboration of the group. Aneuploid reduction in chromosome number and, less frequently the appearance of polyploidy, have

occurred in the evolution of various taxa, apparently connected with the reduction of recombination in ecologically marginal situations.

SYSTEMATIC TREATMENT

Lopezia Cav.

Lopezia Cav., Icon. 1: 12. 1791. Munz, Brittonia 13: 77. 1961; N. Amer. Fl. II. 5: 15. 1965.

Pisaura Bonato, *Pisaura automorpha* e *Coreopsis formosa*, piante nuove. Padova, p. 12. 1793.

Riesenbachia Presl, Rel. Haenk. 2: 36, t. 54. 1831. Type: *R. racemosa* Presl = *Lopezia riesenbachia* Plitmann, Raven & Breedlove. Munz, Brittonia 13: 76. 1961; N. Amer. Fl. II. 5: 15. 1965.

Semeiandra Hook. & Arn., Bot. Beechey's Voy. pl. 59. 1836; 291. 1838. Type: *S. grandiflora* Hook. & Arn. = *Lopezia semeiandra* Plitmann, Raven & Breedlove. Munz, Brittonia 13: 74. 1961; N. Amer. Fl. II. 5: 14. 1965.

Diplandra Hook. & Arn., Bot. Beechey's Voy. pl. 60. 1836; 291. 1838. Nom. cons. prop., Raven & Plitmann, Taxon 20: 648. 1971, Taxon 22: 155. 1973; *non* Bertero, 1830, *nec* Rafinesque, 1840. Type: *D. lopezioides* Hook. & Arn. = *Lopezia lopezioides* (Hook. & Arn.) Plitmann, Raven & Breedlove. Munz, Brittonia 13: 75. 1961; N. Amer. Fl. II. 5: 13. 1965.

Pelozia Rose, Contr. U. S. Natl. Herb. 12: 295. 1909. Type: *P. laciniata* Rose = *Lopezia laciniata* (Rose) M. E. Jones.

Pseudolopezia Rose, Contr. U. S. Natl. Herb. 12: 296. 1909. Type: *P. insignis* Hemsl. = *Lopezia longiflora* Decaisne. Munz, Brittonia 13: 75. 1961; N. Amer. Fl. II. 5: 14. 1965.

Jehlia Rose, Contr. U. S. Natl. Herb. 12: 297. 1909. Type: *Lopezia macrophylla* Benth. = *L. grandiflora* Zucc.

Mostly well branched annual or perennial *herbs*, the perennials sometimes woody and with stems to 1 cm or more in diameter; plants often \pm reddish; stems swollen or underground parts \pm tuberous in some species. *Leaves* cauline, mostly spirally arranged, but sometimes opposite near the base or throughout in some species, reduced upward. *Stipules* present, small, mostly caducous. *Inflorescence* mainly terminal racemes, often leafy at base, more crowded toward apex, corymbose when young or at maturity in a few species, more rarely paniculate; bracts subsessile, narrowly lanceolate or linear, reduced leaves. *Flowers* many, borne on slender, long pedicels, slightly to markedly zygomorphic, often markedly protandrous; floral tube present or absent, the floral parts in any case somewhat united up to a constriction at the summit of the ovary. *Sepals* 4, subequal, narrowly lanceolate. *Petals* 4, subequal or unequal, the upper and lower pairs often markedly dissimilar, the upper 2 petals fused in some species (sect. *Pelozia*) with the upper 3 sepals for part of their length; petals red, purplish, lavender, or white. *Stamens* 2, the lower sterile in all except *L. lopezioides*; staminode petaloid, usually spatulate, \pm enclosing the fertile stamen in many species, and releasing it explosively in sect. *Lopezia*; fertile stamen rotating in nearly mature but from its fundamentally introrse to a fundamentally extrorse position by the twisting of the filament near its end; stamens adnate to style in a few species; anther dorsifixed. *Pollen* blue, yellow in a few species (sects. *Pelozia*, *Riesenbachia*), shed singly. *Stigma* subcapitate, papillose at maturity. Ovary pluriovulate or with one ovule per locule in a few species. *Fruit* a loculicidal, 4-valved

capsule, subglobose or clavate, dehiscent at the apex. *Seeds* many, small, more or less tuberculate, or one per locule in a few species and then larger. Gametic chromosome numbers, $n = 7, 8, 9, 10, 11, 20, 22$; original basic chromosome number, $x = 11$.

TYPE SPECIES: *Lopezia racemosa* Cav.

Distribution: Nearly throughout Mexico and Guatemala, mainly at middle elevations, but absent from the northern deserts and lowland tropics; also in El Salvador, Costa Rica, and Panama.

KEY TO SECTIONS

1. Flowers with two fertile stamens; seeds narrowly winged, 3–4.5 mm long; leaves subopposite Section I. *Diplandra*
1. Flowers with one fertile stamen and a staminode; seeds not winged, ca. 1(–2) mm long; leaves mainly alternate.
 2. Floral tube evident, the stamens and style united to one another and to the lower side of the floral tube Section II. *Riesenbachia*
 2. Floral tube absent, the stamens and style not united except rarely at the very base.
 3. Upper three sepals connate at the base, the petals arising from them; constricted neck at summit of ovary prolonged Section V. *Pelozia*
 3. Sepals not connate; constricted neck at summit of ovary not prolonged.
 4. Flowers bright red, 1 cm or more long; stems swollen just below ground level Section III. *Jehlia*
 4. Flowers purplish, lavender, pinkish, or white, rarely as much as 1 cm long; stems not swollen below ground level in most species.
 5. Wiry-stemmed annual of the northern Sierra Madre Occidental; seeds one per locule; fertile stamen neither tightly enfolded by the staminode nor explosively discharged by it Section IV. *Nannolopezia*
 5. Widespread annual or perennial herbs; seeds usually many per locule; fertile stamen tightly enfolded by the staminode and explosively discharged by it in all but a few populations Section VI. *Lopezia*

KEY TO THE SPECIES

1. Flowers with two fertile stamens; seeds narrowly winged, 3–4.5 mm long; leaves subopposite 1. *L. lopezioides*
1. Flowers with one fertile stamen and a staminode; seeds not winged, ca. 1(–2) mm long; leaves mainly alternate 2
 2. Floral tube evident, the stamens and style united to one another and to the lower side of the floral tube. 3
 3. Flowers (3.5–)4–8 cm long, bright red; soft-wooded shrub, mainly of the pine-oak forest but reaching the upper limits of the tropical deciduous scrub 2. *L. semeiandra*
 3. Flowers less than 1 cm long, lilac-violet or purplish to bluish-pink; annual herb; relatively low elevations in tropical deciduous scrub 3. *L. riesenbachia*
 2. Floral tube absent, the stamens and style not united except rarely at the very base 4
 4. Upper three sepals connate at the base, the petals arising from them; constricted neck at summit of ovary prolonged 5
 5. Upper petals laciniate, white with red veins; pollen blue; capsule obovoid-obconical or subglobose 6
 6. Stoloniferous perennials 1–6 dm tall; some leaves longer than 3 cm; sepals 3.5–7 mm long; capsule obovoid-obconical, more or less puberulent 18. *L. laciniata*
 6. Annual herbs 0.6–2.5 dm tall; leaves shorter than 3 cm; sepals 3–4.5(–5) mm long; capsule subglobose, setose or setose-tuberculate 19. *L. gentryi*
 5. Upper petals not laciniate, pink; pollen yellow; capsule subcylindrical 7
 7. Main leaves subentire; upper petals lanceolate; staminode ca. 5 mm long; capsule ca. 3 mm thick; seeds transversely tuberculate, black; Sinaloa 21. *L. sinaloensis*

20. Upper petals without a conspicuous gland; seeds transversely rugose-tubercled; leaves mostly opposite; Sinaloa, Mexico 15. *L. conjugens*
20. Upper petals with a conspicuous gland; seeds muricately tuberculate; leaves alternate, rarely a few opposite; wide-spread 14. *L. racemosa*

Section I. *Diplandra*

Lopezia sect. *Diplandra* (Hook. & Arn.) Plitmann, Raven & Breedlove, comb. nov.

Diplandra Hook & Arn., Bot. Beechey's Voy. 291, pl. 60. 1838. Nom cons. prop., Raven & Plitmann, Taxon 20: 648. 1971; Taxon 22: 155. 1973; non Bertero, 1830, nec Rafinesque, 1840. Munz, Brittonia 13: 75. 1961; N. Amer. Fl. II. 5: 13. 1965.

Virgate woody *perennial*, the stems swollen just below the level of the ground. *Leaves* mainly opposite, some of the lower ones alternate. Inflorescence terminal, corymbose in flower, racemose in fruit. *Flowers* strongly protandrous, the parts free. *Sepals* subequal, the upper 3 ascending-divergent. *Petals* red, the upper ones larger than the lower ones. *Stamens* both fertile, equal or the upper one shorter. *Anthers* introrse. *Nectaries* massive. *Pollen* pale violet-blue. *Capsules* subglobose, opening to the middle, with one seed in each locule. *Seeds* 4, broadly oblong, flattened, narrowly winged. Gametic chromosome number, $n = 11$.

TYPE SPECIES: *Lopezia lopezioides* (Hook. & Arn.) Plitmann, Raven & Breedlove.

Distribution: Known only from the pine-oak-madroño forests of a few volcanic mountains in northwestern Jalisco and south and central Nayarit, Mexico, at elevations of 1400 to 2000 or 2500 m.

This highly isolated relict species is one of the most interesting in the family Onagraceae. It occurs only in a few localities in the Sierra Madre Occidental at its junction with the Trans-Mexican Volcanic Belt. It is unique within the *Lopezieae* in its possession of two fertile stamens.

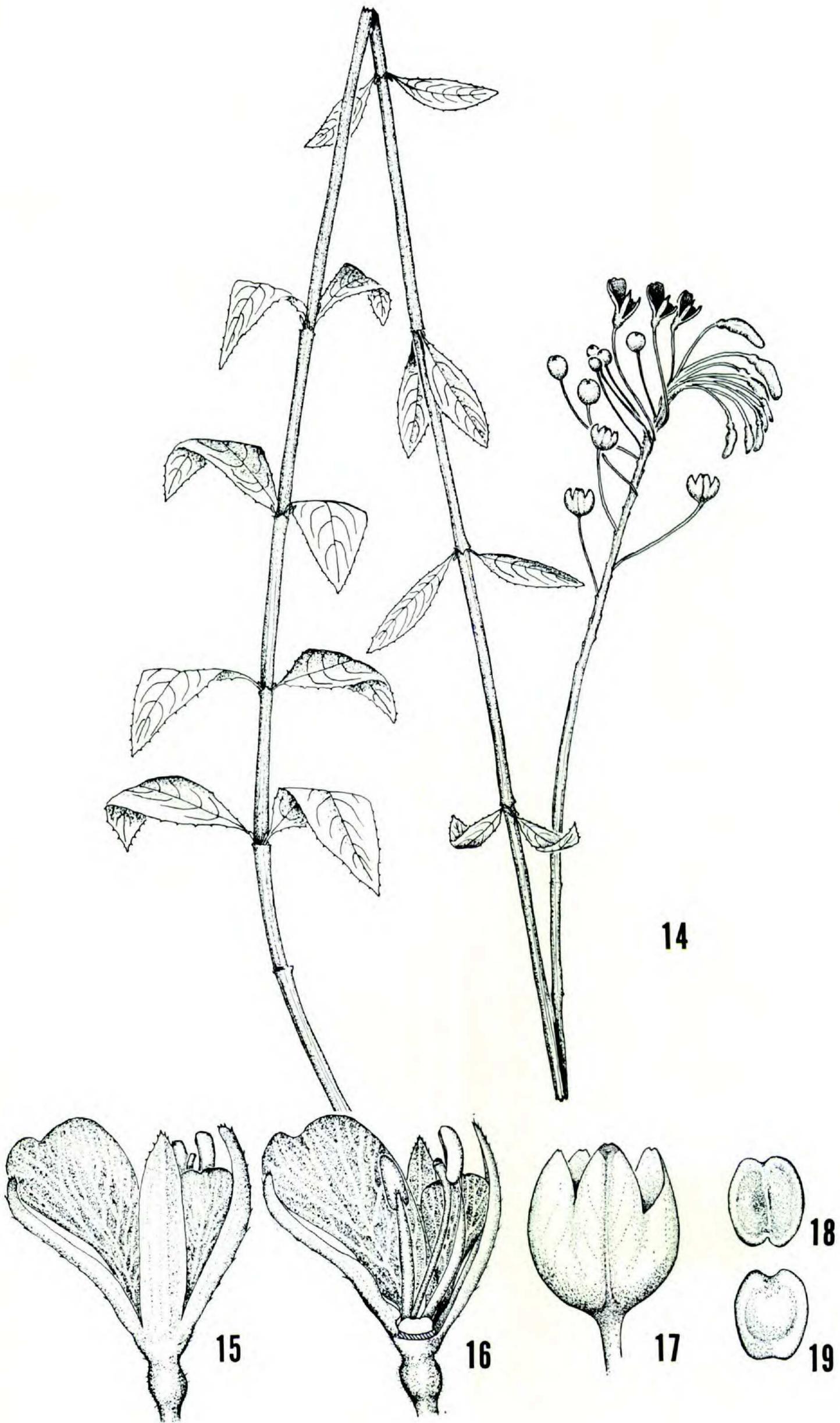
1. *Lopezia lopezioides* (Hook. & Arn.) Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 281. 1973.—FIGS. 14–19.

Diplandra lopezioides Hook. & Arn., Bot. Beechey's Voy. pl. 60. 1836; 292. 1838. Munz, Brittonia 13: 76. 1961; N. Amer. Fl. II. 5: 14. 1965.

Stems 10–30 dm tall, hirsute to glabrescent. *Leaves* hirsute to hirtellous; lower leaves (3–)4–11 cm long and 1.1–3.2 cm wide, oblong-elliptic to lanceolate, cuneate or attenuate at base, acute or acuminate at the apex, infrequently obtuse or even retuse, serrate or serrulate, ciliolate, with 7–15(–20) veins on each side of

→

FIGURES 14–19. *Lopezia lopezioides*.—14. Stem and inflorescence, $\times 0.5$.—15. Flower, $\times 2.8$.—16. Flower with one sepal and two petals removed, $\times 2.8$.—17. Capsule, $\times 2.8$.—18. Seed, adaxial view, $\times 2.8$.—19. Seed, abaxial view, $\times 2.8$. All from *Breedlove 8052* (DS).



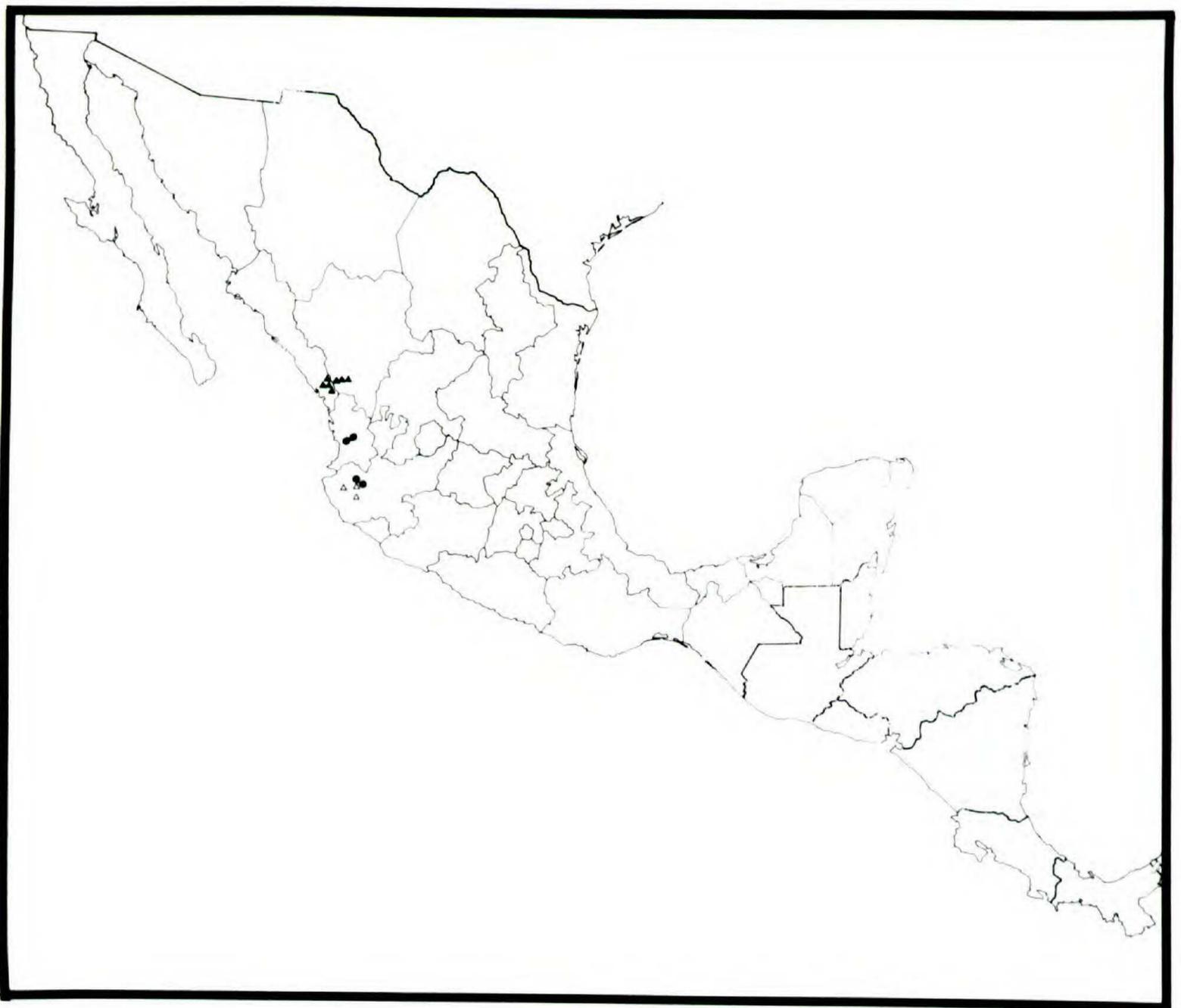


FIGURE 20. Geographical distribution of *Lopezia lopezioides* (dots), *L. laciniata* subsp. *laciniata* (open triangles), and *L. laciniata* subsp. *ovata* (filled triangles).

the midrib; upper leaves 0.9–3 cm long and 0.3–0.8 cm wide, lanceolate or linear-elliptic, acute to rounded at base, subacute at apex, serrulate to entire, with 5–10 veins on each side of the midrib; petioles 0–1.2 cm long. *Inflorescence* glandular-pubescent; pedicels 20–45 mm long, ascending or spreading, \pm puberulent. *Sepals* 10–16 mm long, and ca. 2 mm wide, \pm densely hirtellous and glandular-pubescent, the upper three ascending-divergent, the lower a little longer, somewhat incurved. *Petals* red, the upper ones 8–10 mm long and 4–5 mm wide, obovate, cuneate attenuate at base, truncate to retuse, the lower ones 4–7 mm long and 2–3 mm wide, oblong-ob lanceolate, attenuate at base \pm obtuse. *Stamens* 7–11 mm long; filaments 5–9 mm long; anthers 2.5–4 mm long. *Style* 5–9 mm long, ca. 0.5 mm thick; stigma ca. 1 mm in diameter; ovary 1.5–2 mm long, subglobose, puberulent. *Capsule* 7–12 mm long, 5–9 mm thick, puberulent to glabrescent; valves coriaceous, ovate, dentate-retuse at apex. *Seeds* 3–4.5 mm long, retuse at both ends. Gametic chromosome number, $n = 11$.

Type: Mexico, Nayarit, Tepic, 1827–28, *F. W. Beechey* (K; photograph, MICH).

THE MATERNAL POUCH AND DEVELOPMENT IN THE MARSUPIAL FROG *GASTROTHECA RIOBAMBAE* (FOWLER)

EUGENIA M. DEL PINO, MARIA L. GALARZA, CARMEN M. DE ALBUJA,
AND A. A. HUMPHRIES, JR.

*Instituto de Ciencias, Pontificia Universidad Catolica del Ecuador, Quito, Ecuador and
Department of Biology, Emory University, Atlanta, Georgia, 30322*

Gastrotheca riobambae (Fowler) is a common frog in the northern interandean valleys of Ecuador. In this genus, after the eggs leave the female's cloaca, the male places them inside a dorsal pouch in the body of the female (Walker, 1957; Matthews, 1957) where the embryos develop until the tadpole stage. Spannhof and Spannhof (1972), working with *Gastrotheca marsupiata*, found that incubation of embryos in the pouch lasts approximately five to six weeks, but the larvae may remain in the pouch for considerably longer periods, depending on environmental factors. After leaving the pouch, the tadpoles continue their development in water, where metamorphosis occurs in a few weeks. Hoogmoed (1967) has studied the mating and early development of *Gastrotheca marsupiata* and reviewed most of the existing literature. Additional observations on the embryonic incubation and larval development of *Gastrotheca marsupiata* have been reported by Spannhof and Spannhof (1972). Recent studies of the taxonomy and distribution of *Gastrotheca* in South America resulted in the conclusion that the populations of this genus in the vicinity of Quito are primarily *Gastrotheca riobambae* (Duellman and Fritts, 1972; Duellman, 1974). Although reports dealing with the pouch and reproductive activity of *Gastrotheca riobambae* are limited to the paper of Jones, Gerrard and Roth (1973), it is possible that some descriptions, such as those of Hoogmoed (1967), are actually based on *G. riobambae*, rather than *G. marsupiata*, since the animals were collected near Quito.

The maternal pouch of *Gastrotheca* is of uncommon interest as an adaptation to life on land, but surprisingly little is known about it. Experimental induction of pouch formation in juvenile females of *Gastrotheca riobambae* has been studied (Jones *et al.*, 1973), and aspects of the histology of the pouch of *Gastrotheca marsupiata* have been described (Spannhof and Spannhof, 1972); but the details of the histology and physiology of the pouch and the processes of embryonic development in the pouch have not yet been thoroughly studied. In this report we present the initial results of a study of reproduction in *Gastrotheca riobambae*, with particular emphasis on the structure of the pouch and embryos, maternal-embryonic relationships and changes in the pouch related to reproductive activity.

MATERIALS AND METHODS

Adult specimens of *Gastrotheca riobambae* were collected in Quito, Ecuador, on the grounds of Pontificia Universidad Catolica del Ecuador, from other localities within the city, and near Machachi, a town located approximately 50 km south of Quito. The animals were brought into the laboratory and kept in a $1.50 \times 0.40 \times$

0.60 m terrarium. The terrarium was provided with vegetation and a tray containing pond water and several stones which gave supporting surfaces for the females at the time of tadpole hatching and emergence from the pouch. Both brown and green variants of the species were common at the collection sites and frogs of both colors were used for this study. Observations are based on a total of more than 50 frogs.

Ovulation was induced by the administration of 800 IU of human chorionic gonadotropin (Coriantin, Richter) into the coelomic cavity of the female. Males were stimulated to mate by the similar administration of 100 to 200 units. Mating occurred 24 hours or more after hormone administration. As stated, mating occurs on land, and, as they emerge from the cloaca, the eggs are moved into the pouch by the male. Sometimes only the female responded to the hormone treatment and in such cases the eggs released were not placed in the pouch but instead were deposited and left on the ground.

Pouch and embryos were fixed in Bouin's picro-formol, embedded in paraffin and cut into sections of 10 μ m thickness. Harris hematoxylin and alcoholic eosin yellow were used for routine staining. Whole mount permanent preparations of embryos were made by cutting the embryos from the yolk, fixing them in Bouin's and staining them with borax-carmine.

Eggs and embryos from the pouch were cultured in pond water or in several concentrations of amphibian Ringer's solution.

RESULTS

General morphology of the pouch

The pouch is a sac underlying the dorsal integument, but is essentially independent of it except at the aperture. Histologically, the pouch resembles amphibian integument, but differs significantly from it, particularly during reproduction. The pouch is absent in males and juvenile females, but is always present in the sexually mature female. The aperture of the pouch is triangular, with the apex of the triangle directed anteriorly (Fig. 1). The entrance to the pouch can be open or closed, depending on the stage of the reproductive cycle. In open pouches, the borders of the aperture are wide apart, giving a broad triangular or "U" shape (Fig. 1), whereas in the closed condition the borders of the aperture join in the midline of the body, giving a slit-like appearance (Fig. 2). The pouch aperture remains open after tadpole birth and throughout the growth of the next generation of oocytes in the ovary. Closure ordinarily occurs when the ovarian eggs have attained their full size just before the time of ovulation, but in females with large ovaries, closure can be induced experimentally in about twelve hours by injection of chorionic gonadotropin. The pouch remains closed during the time the embryos are being incubated, but even during this period it is easy to gain access to the pouch with a blunt probe or forceps for the removal of embryos. Under ordinary conditions, opening of the pouch occurs when the tadpoles are ready for hatching and release; we have observed, however, that handling of a frog with a closed pouch results in an immediate opening of the pouch. Following such an opening, if the animal is left undisturbed, the aperture closes again in about an hour.

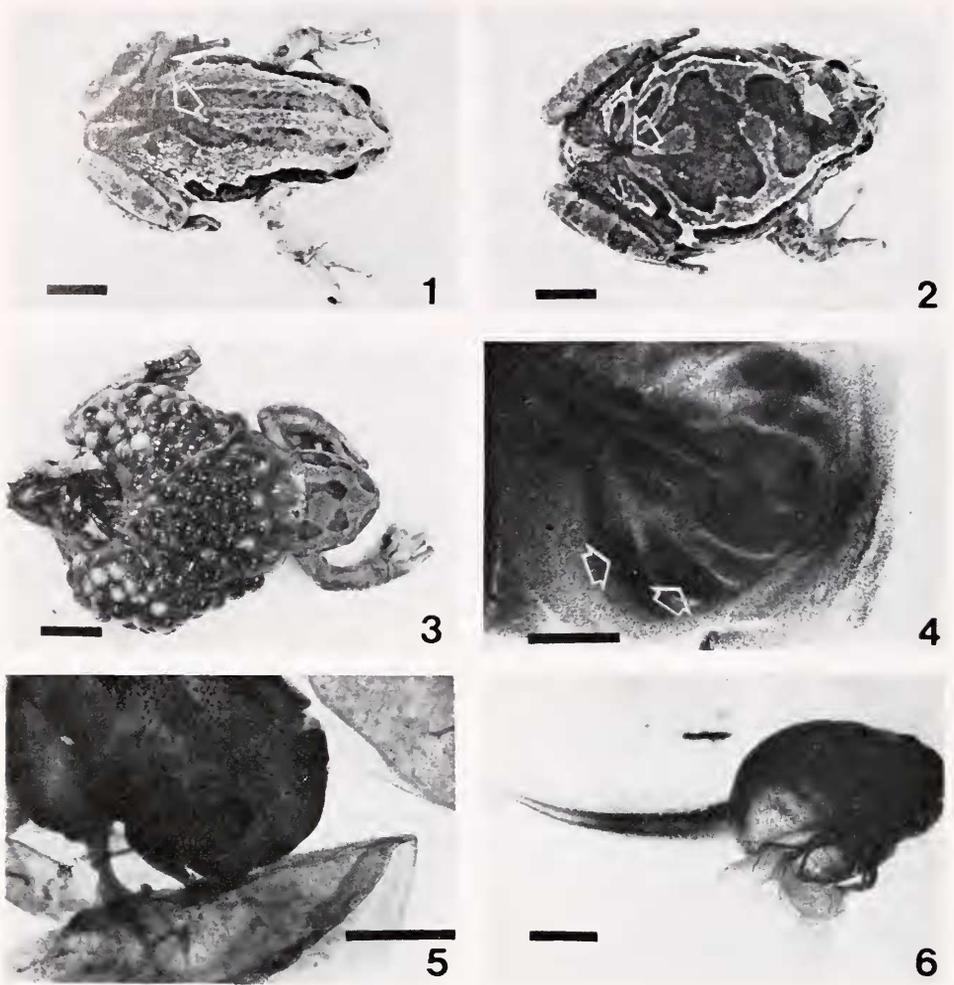


FIGURE 1. Female *Gastrotheca riobambae* before mating. The pouch aperture is open. Pouch aperture is triangular in shape, with the apex of the triangle (arrow) directed anteriorly. Bar represents 1 cm.

FIGURE 2. Female with developing embryos in the pouch. The pouch is considerably distended, with its anterior limit reaching almost to the head (solid arrow). The aperture of the pouch is closed and slit-like (open arrow). Bar represents 1 cm.

FIGURE 3. Female with developing embryos in the pouch. The dorsal integument has been removed to expose the intact distended pouch with the embryos inside. The pouch is almost transparent and fills the entire dorsal and lateral sides of the body. Bar represents 1 cm.

FIGURE 4. Early embryo removed from the pouch. The yolk was dissected and the embryo was prepared as a whole mount. The primordia of the bell gills are noticeable on both sides of the head (arrows). Bar represents 500 μ .

FIGURE 5. Advanced embryo removed from the pouch and jelly capsule (whole mount permanent preparation). The bell gills are large discs that in the living condition completely enveloped the embryo. Each gill is connected to the body by means of gill stalks (arrow). Bar represents 500 μ .

The pouch is attached to the integument and to the part of the body lying ventral to the pouch by thin lateral ligaments carrying blood vessels and nerves. In addition, there are long thread-like structures lying in the midline, carrying vessels and possibly nerves, which connect both the ventral and dorsal walls of the pouch with the area ventral to it. There is a sheet of muscle on the dorsal side, extending between the integument and the pouch. Although the pouch is a permanent structure, it varies considerably in size, depending upon the phase of reproduction. In nonpregnant females (*i.e.*, females without eggs in the pouch), the pouch extends approximately 1 cm anteriorly and laterally from the aperture. The pouch of the pregnant female becomes highly distended as the embryos develop, extending approximately 3 cm anteriorly from the aperture and bringing the limits of the fully-distended pouch anteriorly to the base of the head and laterally into the ventral portions of the body (Figs. 2 and 3). The distension of the pouch at this time is such that its walls become almost completely transparent (Fig. 3), in contrast to the essentially opaque condition of the nonpregnant pouch.

Structure of the nonpregnant pouch and changes during reproduction

The histological structure of the pouch before ovulation resembles that of amphibian integument. The pouch is lined with stratified squamous epithelium, which is closely associated with numerous simple alveolar mucous glands, usually with large lumina. Some glands have small lumina, and the cells of these glands are considerably swollen with accumulated secretory material. A few scattered serous glands are present. As compared with the skin, the pouch contains fewer mucous and serous glands, and its epithelium is thrown into numerous folds at this stage (Fig. 7). The pouch epithelium also appears less keratinized than the epithelium of the skin. Just below the basal membrane, chromatophores and sometimes small blood vessels are seen. The corium is thick, with scattered large blood vessels located deep within it. The part of the corium immediately below the basal membrane is loosely arranged and serves as a matrix for the glands, while the deeper layer contains dense fibers of connective tissue in parallel bundles, as well as some elastic fibers. A layer of muscle can sometimes be seen below the corium. The outer limit of the pouch is formed by a layer of mesothelium.

Only one female was studied for changes immediately following ovulation without mating, but in this animal the most noticeable difference between her pouch and pouches observed before ovulation was in the mucous glands. The lumina of these glands tended to be occluded by the enlarged secretory cells (Fig. 8), in contrast to their condition before ovulation. No change was detected in the number of glands. Folds were conspicuous in the epithelium.

Ovulation is usually followed by mating and filling of the pouch with eggs. The initial changes associated with incubation of the eggs appear to be the development of activity in the mucous glands and the thinning of the pouch. Enlargement of the pouch seems to be the result of the presence of eggs, presumably due to

FIGURE 6. Living embryo of an advanced stage removed from the pouch and the jelly capsule. Before the jelly was removed, the gills completely enveloped the embryo, but removal resulted in collapse and shrinkage of the gills. The blood vessels within the gill stalks are prominent. Bar represents 2 mm.

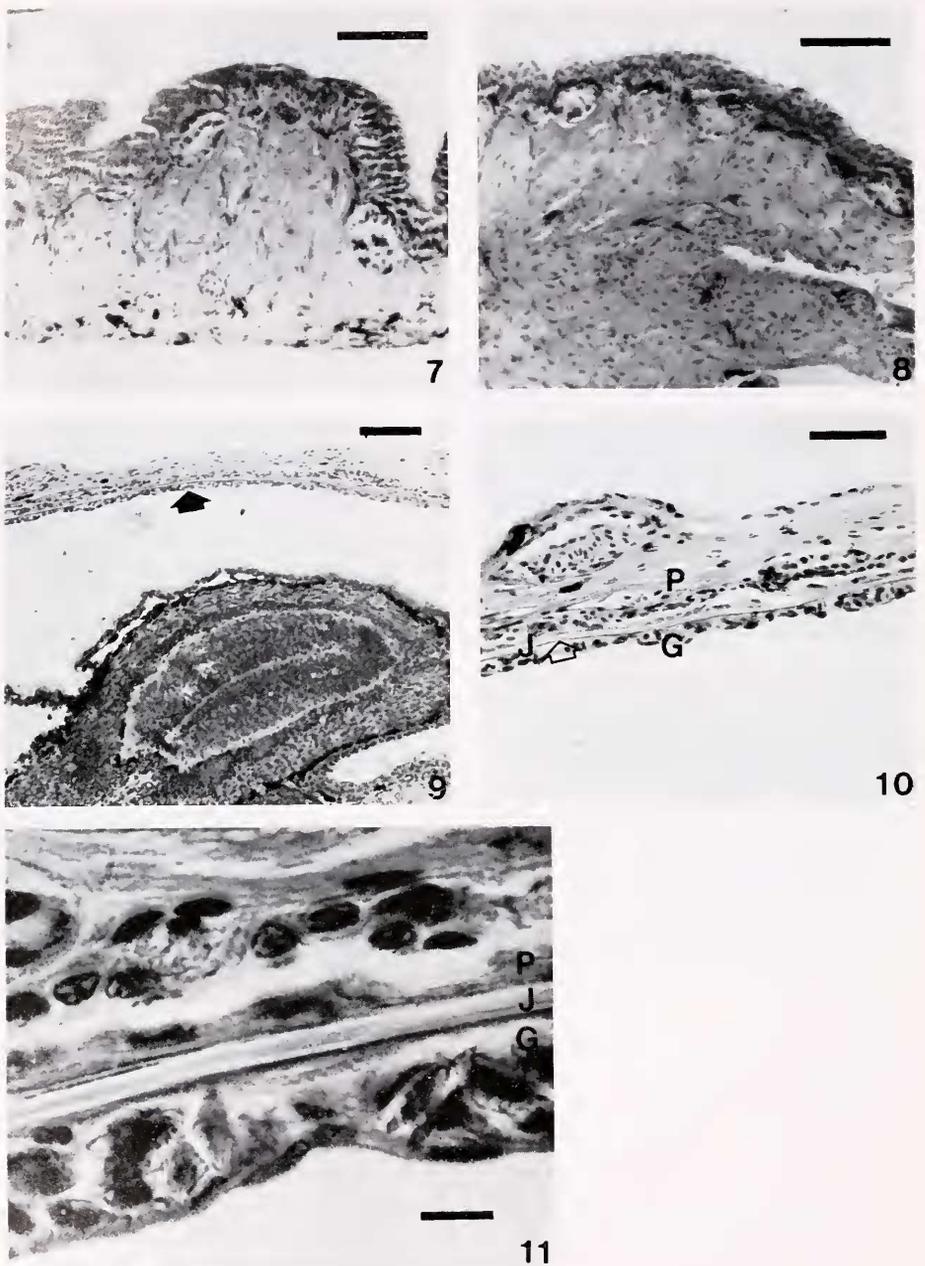


FIGURE 7. Cross section of the pouch before ovulation. Infoldings of the epithelium are prominent, and there are numerous simple alveolar glands with empty lumina. The epithelial layer is less keratinized than the integument, but the general appearance is similar. Bar represents 100 μ .

mechanical distension, since we observed that in one female that oviposited but did not mate, the pouch remained the same size fifteen days after egg laying.

Embryonic development in the pouch is accompanied by increased vascularization of the pouch lining and close association between pouch and egg jelly (Figs. 9, 10 and 11). As the pouch walls become thinner, numerous blood vessels invade the area of the basal membrane and therefore come to lie very close to the epithelium (Figs. 10 and 11). The mucous glands have large lumina and are rare, compared to the previous condition. Initially, the walls of the pouch are in simple contact with the jelly capsules of the embryos, but as development proceeds, each encapsulated embryo comes to be partially enclosed in a vascularized pocket of pouch tissue. The chambers are formed by the upper and lower walls of the pouch and by lateral projections from these walls around the embryos.

Embryonic incubation in the pouch ends with hatching and release of the tadpoles. Birth of the tadpoles is followed by shrinkage and thickening of the lining of the pouch. Immediately after birth, the egg pockets of the pouch are still present but are collapsed (Fig. 12); the pouch appears disorganized when compared with that of the pregnant female.

Regression of capillaries in the pouch follows the birth of the tadpoles and the projections which formed the embryonic chambers are withdrawn. Epithelial folds are prominent immediately following birth (Fig. 12), but reorganization of pouch tissue eliminates them either by invagination of the epithelium, followed by tissue reorganization within the layer of connective tissue, or by evagination and shedding. Extensive shedding of the epithelium was noticed some days after birth of the tadpoles. During reorganization, numerous compound alveolar glands with large lumina appear, located deep in the layer of connective tissue (Fig. 13).

In a female examined fifty-two days after birth of the tadpoles, the structure of the pouch appeared similar to that of the sexually mature female before ovulation, but epidermal folds were inconspicuous. Mucous glands were present but were of the simple alveolar type, with large lumina.

Embryonic incubation and birth of tadpoles

Early development, occurring inside the pouch, is essentially synchronous. Development is associated with an increase in size of the embryos, and the pouch becomes much expanded as development proceeds. Segmenting eggs taken from the pouch are approximately 3 mm in diameter and are covered by a thin but firm coat of jelly; they lack dark pigment and the yolk gives them a rather uniform

FIGURE 8. Cross section of the pouch immediately after ovulation. No eggs had been placed in the pouch. The pouch is similar to that prior to ovulation except for the mucous glands, whose cells appear to be enlarged with accumulated secretory material. Bar represents 100 μ .

FIGURE 9. Cross section of an embryo within the pouch. The embryo is surrounded by the fluid-filled space of the capsule. The bell gill (arrow) is flattened against the jelly, and the jelly lies against the vascularized tissue of the pouch. Detail is shown in the next two figures. Bar represents 100 μ .

FIGURE 10. Detail of association between bell gill (G), jelly (J), and pouch (P). Bar represents 50 μ .

FIGURE 11. Higher magnification of the gill-jelly-pouch relationship shown in Figure 10. Bar represents 10 μ .

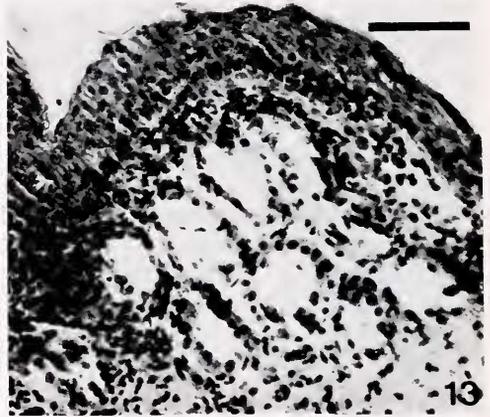
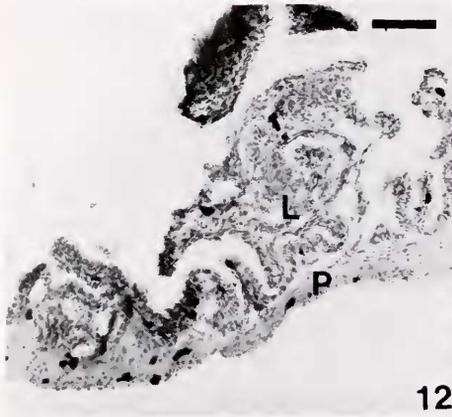


Figure 12. Pouch immediately following hatching and emergence of the tadpoles. The extensive folding and vascularization of the lining is evident. Bar represents 100 μ .

FIGURE 13. Reorganizing pouch 27 days after emergence of the tadpoles. Note the presence of a compound alveolar gland. Bar represents 100 μ .

FIGURES 14 AND 15. Cross section of two adjacent embryos within the pouch. Each embryo is associated with the epithelium of the pouch, but the jelly capsules of the two embryos were probably contiguous with each other before shrinkage was induced by fixation. P represents pouch; open arrows, jelly; solid arrows, gill. The bar in Figure 14 represents 100 μ ; bar, Figure 15, represents 50 μ .

yellowish-white color. The first cleavage divisions appear to divide the egg into four large blastomeres, but it is not known whether the cleavage furrows in the vegetal area are more than superficial. Development occurs at the animal end of the egg in a manner, described by Spannhofer and Spannhofer (1972), as similar to that

of a fish. The early development of *Gastrotheca riobambae* in the pouch is indeed different from that described for anurans such as *Xenopus laevis* or *Rana pipiens* (Nieuwkoop and Faber, 1967; Rugh, 1962). A unique developmental characteristic of *Gastrotheca* is the early appearance and subsequent marked growth of a pair of expanded gills, called "bell gills" (Noble, 1927). These gills originate from two paired masses of tissue, the gill primordia, located on either side of the head of the early embryo (Fig. 4). The functional gills of *Gastrotheca* originate from the fusion of these two primordia on each side. In the early gills the area of fusion of the two primordia, indicating their double origin, is easily distinguished. Later, the gills become small vascularized discs; still later, when fully developed (Figs. 5 and 6), they completely surround the embryo, with the right and left gills joining to form a highly vascular sac in intimate contact with the inner surface of the jelly coat (Figs. 9, 10, and 11). Each gill is connected to the embryo-proper by two long vascular stalks (Fig. 6); each stalk consists of one efferent vessel and one afferent vessel within a common membranous covering. Therefore, between each gill and the embryo there are four connecting blood vessels. Later in development, the gills appear to cease growth, thus at the time of hatching and birth, since the embryo has continued to grow, the gills no longer envelop the entire embryo. Although the gills appear simply to halt their growth, it is possible that they may actually decrease in size toward the later stages of development. At hatching, the vascularized discs of both gills protrude through the left operculum, but the gill stalks have been retracted and are no longer visible externally. Immediately after birth the gills are bright red; after a few minutes of contact with pond water, however, the red color disappears. Apparently the circulation through the gills stops soon after hatching, after which gill resorption occurs, taking approximately 24 hours. The histological constitution of the fully developed bell gill (Figs. 9, 10, 11, 14, and 15) appears as a thin epithelium containing numerous blood vessels associated with the basal membrane. The gills bear a general resemblance to lung tissue.

During the initial stages of embryonic development there is minimal association between pouch and embryos; young embryos can readily be extruded to the outside by slight external pressure on the pouch. As development continues, however, removal of embryos becomes somewhat more difficult. The increased difficulty of removal is due to the development of an intimate association between the gills of the embryo and the highly vascular lining of the pouch, with only the thin layer of jelly lying between the maternal and embryonic circulation (Figs. 9, 10, and 11).

Embryos may be distributed in the pouch in either a single or a double layer. In all cases, however, each embryo is in contact with pouch lining. Ordinarily, embryos do not seem to be completely enveloped by pouch tissue, although this might conceivably occur when there are few embryos in the pouch. Each embryo lies in an individual concavity of pouch tissue and in close contact with it, but the jelly of some embryos is contiguous (Figs. 14 and 15). In this situation, therefore, the vascular systems of adjacent embryos are separated from each other by their thin jelly capsules only.

The period of incubation within the pouch is somewhat variable. Under laboratory conditions we have observed a range of 103 to 120 days. Hatching usually

occurs in the pouch, followed by emergence aided by the mother. Just before emergence of the tadpoles, the female moves into water and rests her forelegs on a supporting surface. She then inserts the long toes of her hind legs into the pouch and, after a few seconds, one or two swimming tadpoles emerge. The female usually remains motionless for less than a minute before repeating the insertion process. In the laboratory, on occasion, not all the tadpoles from a female hatched on the same day, but rather over a period of two or more days.

The number of embryos per pouch varies considerably: in 11 females, the number ranged from 81 to 207, with a mean of 125 ± 10 (s.e.). Unfertilized eggs or dead embryos in the pouch were rare, but when present, they had dried in the pouch and were expelled with the newly hatched tadpoles at the time of birth. Measurements of 42 newly hatched tadpoles from 8 females gave a snout to vent length of 7.7 ± 0.2 mm, with a total length of 20.2 ± 0.4 mm.

Segmenting eggs and very early embryos within the jelly do not survive in pond water but can be cultured in Ringer's solution for as long as seventeen days. Embryos cultured in Ringer's solution without aeration develop more slowly than those left in the pouch and appear to be deficient in blood formation. Aeration of the solution increases developmental rate and seems to improve blood production. Escape from the jelly does not occur in segmenting eggs and early embryos cultured *in vitro*, but advanced embryos hatch soon after being placed in pond water or Ringer's. Pouch embryos that have acquired the tadpole shape and have developed complete bell gills (Fig. 6) can be cultured either in pond water or Ringer's. In either medium, they soon hatch from the jelly and appear as very small free-living tadpoles. Resorption of the bell gills usually takes several days under these conditions.

As mentioned earlier, circulation through the bell gills apparently ceases soon after normal hatching, after which the gills are resorbed. If hatched tadpoles are kept in $1.5\times$ Ringer's solution, however, the circulation and gills are maintained. Free-living tadpoles can be equally well maintained in pond water or in Ringer's solution.

DISCUSSION

Reproductive adaptations toward a terrestrial mode of life have evolved in a number of amphibian groups. Among the anurans, *Nectophrynoidea occidentalis* shows true viviparity (Angel and Lamotte, 1948). Others have not gone that far, but have abbreviated the aquatic dependence for embryonic development in many different ways (cf. Gallien, 1959; Noble, 1931). Members of the genus *Gastrotheca* are examples of the latter group. In this genus the requirement of an aqueous environment for embryonic development has been diminished or essentially eliminated, depending on the species. In *Gastrotheca ovifera*, young metamorphosed froglets are born from the pouch, while in *Gastrotheca marsupiata* and *Gastrotheca riobambae*, tadpoles are born (Matthews, 1957; Hoogmoed, 1967; Spannhof and Spannhof, 1972; this paper). In this latter case, the tadpoles metamorphose after only a few weeks of aquatic development. Mating in *Gastrotheca* occurs on land, in contrast to the more usual situation for anurans.

In evolution, the pouch of *Gastrotheca* may have originated as a fold of dorsal skin serving to protect the embryos in a terrestrial environment. One may suppose that the pouch could have served originally as a structure protecting the embryos against predation; at the same time, the surrounding tissue would also insure the embryos against desiccation. It may be that the pouch of *Gastrotheca* originated as shallow folds of skin similar to those bordering the egg mass carried on the back of the female *Fritziana* (see Trueb, 1974, for a discussion of the possible phyletic relationship of the South American pouched frogs). Development of the pouch (Jones *et al.*, 1973), which involves invagination of the integument, is in agreement with that idea.

Noble (1925) found that, in the Amphibia, reduction of functioning of the lungs is correlated with modifications of the skin which make it more effective in respiration. One of the modifications involves the penetration of capillaries from the dermis into a closer association with the epidermis. According to Noble, these capillaries lie just beneath the outermost epidermal layer. In a similar way, the vascularization lying close to the epithelium of the pouch in *Gastrotheca* during pregnancy, together with the general thinning of the pouch wall, appear to transform the pouch of pregnant females into an organ functioning in gaseous exchanges between mother and embryos. Noble (1925) mentioned the pouch as a specialized respiratory organ, and Spannhof and Spannhof (1972) observed not only the vascularization of the pouch in *G. marsupiata* but also the formation of egg chambers. We have seen what is apparently a similar situation in *G. riobambae*. It seems evident that the vascularization of the outgrowths forming the egg chambers enhances the capacity of the pouch for gaseous exchange. The maternal and embryonic circulatory systems are separated only by the thin (about 10 μ) jelly capsule of the embryo, and this may be assumed to be of little hindrance to diffusion of gases.

In addition to the rather obvious respiratory function of the pouch, it is also possible that maternal-embryonic exchanges of water and/or other materials may occur between the closely apposed circulatory systems. Jones *et al.* (1973) support the idea of maternal-embryonic interchanges, but without reference to the nature of the materials supposedly exchanged and without specific evidence. Spannhof and Spannhof (1972), on the other hand, believe that probably no nutrient transfer occurs in the pouch, since they were able to maintain embryos and follow development for as long as 8 days outside the pouch. Evidence from the present study confirms the fact that embryos can be cultured outside the pouch for extended periods under certain conditions, but is of no help with regard to the matter of maternal-embryonic exchanges. Preliminary studies in our laboratory, however, reveal no appreciable change in the dry weight of embryos while in the pouch, suggesting that there is not a passage of nutrients from the mother into the embryo.

Hormonal factors are evidently important in pouch formation and function. Pouch formation has already been shown to be elicited by injection of estradiol into immature females (Jones *et al.*, 1973). Our observations suggest a hormonal role in opening and closing of the pouch aperture. It is possible that embryonic incubation, together with vascularization of the pouch and the formation of egg chambers, may also be under hormonal control. Preliminary experiments in our

laboratory, using ovariectomized pregnant females, give support to this possibility. Pouch function, at least insofar as opening and closing of the aperture is concerned, seems also to be subject to nervous control. This is manifest in the rapid opening of the pouch aperture when a pregnant female is handled.

The embryonic bell gills of *Gastrotheca*, along with the pouch, are clearly important adaptations in terrestrial reproduction, and it is worth noting that most frogs with incubating pouches develop this type of gill (Noble, 1931). The evidence of the present study indicates a double origin of the gills, as does the work of Spannhof and Spannhof (1972), who traced the origin of the blood vessels of the gills of *Gastrotheca marsupiatata* to the first and second aortic arches. The gills of *Gastrotheca* might have been multiple originally, similar to the situation in some species of *Cryptobatrachus* (Noble, 1927).

The study of reproduction in *Gastrotheca* is of considerable interest for comparative physiology, development and anatomy, as well as for the general problem of evolutionary adaptations to the terrestrial environment. In this case, the pouch and the pattern of development, along with associated hormonal and nervous control systems constitute remarkable modifications which make possible an extended period of independence from the aquatic environment. Further study of the details of reproduction in this species is in progress.

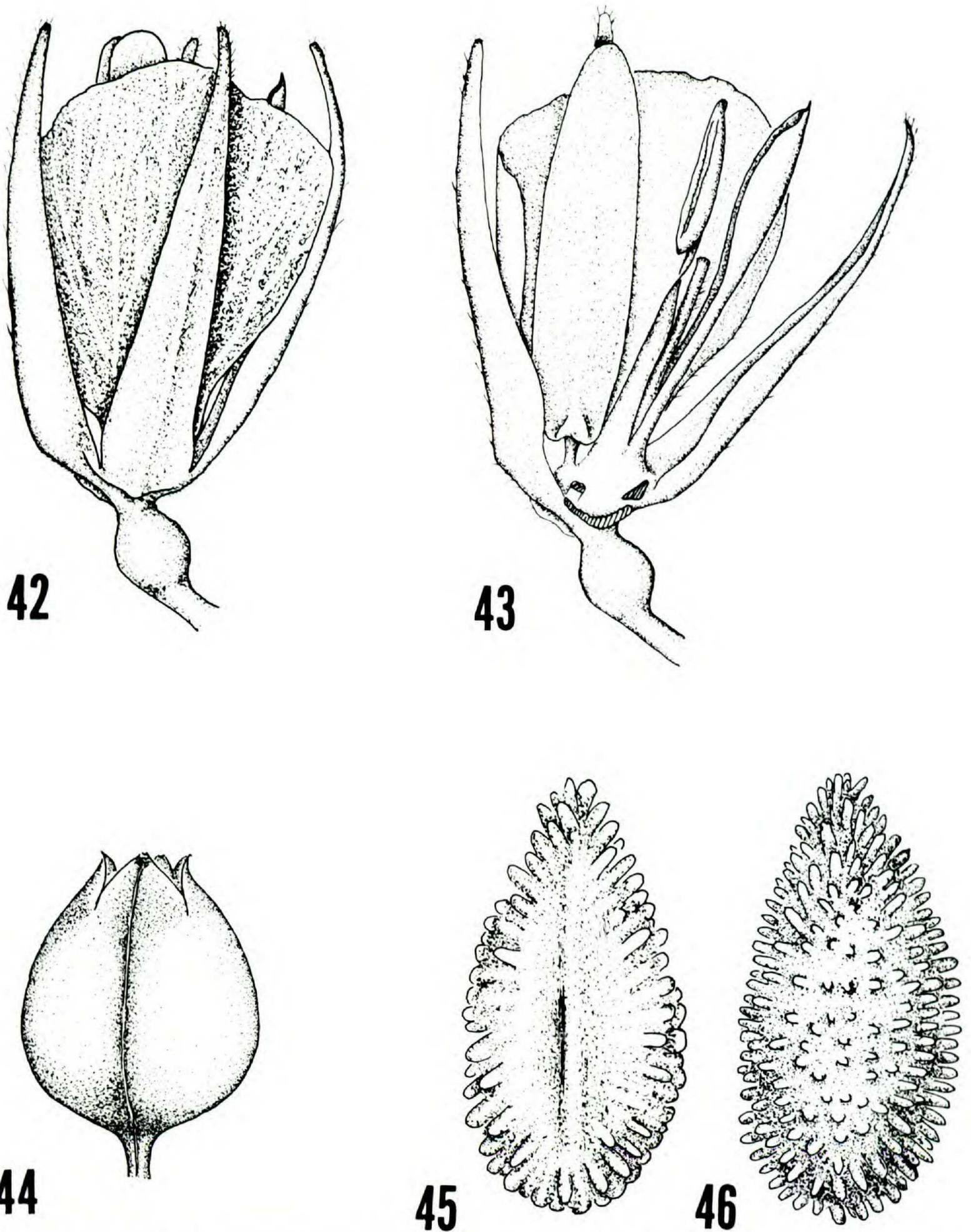
SUMMARY

The pouch of *Gastrotheca riobambae* (Fowler) serves as the location for development of the embryo up to the swimming tadpole stage. The pouch lies under the dorsal integument of the female and, in nonpregnant females, is similar to the integument. Pregnancy is accompanied by increased vascularization of the pouch. Blood capillaries from the corium become closely associated with the epithelial lining of the pouch, and vascularized outgrowths of the pouch partially envelop the embryos. Embryonic development in the pouch is characterized by the presence of peculiar gills, the highly vascularized "bell gills," which expand and flatten against the inner surface of the jelly capsule, forming an individual sac about each embryo and thus establishing a close relationship between embryonic and maternal circulatory systems. After birth of the tadpoles, the gills are soon resorbed and there is regression of the vascularization of the pouch. Reorganization of the tissue and shedding of the lining epithelium restore the pouch to the condition found in the nonpregnant female.

LITERATURE CITED

- ANGEL, F., AND M. LAMOTTE, 1948. Nouvelles observations sur *Nectophrynoides occidentalis* Angel. Remarques sur le genre *Nectophrynoides*. *Ann. Sci. Natur. Zool. Biol. Anim.*, 10: 115-147.
- DUELLMAN, W. E., 1974. A systematic review of the marsupial frogs (Hylidae: *Gastrotheca*) of the Andes of Ecuador. *Occas. Pap. Mus. Natur. Hist. Univ. Kansas, Lawrence*, 22: 1-27.
- DUELLMAN, W. E., AND T. H. FRITTS, 1972. A taxonomic review of the southern Andean marsupial frogs (Hylidae: *Gastrotheca*). *Occas. Pap. Mus. Natur. Hist. Univ. Kansas, Lawrence*, 9: 1-37.
- GALLIEN, L., 1959. Endocrine basis for reproductive adaptations in Amphibia. Pages 479-487 in A. Gorbman, Ed., *Comparative endocrinology*. John Wiley and Sons, New York.

- HOOGMOED, M. S., 1967. Mating and early development of *Gastrotheca marsupiata* (Dumeril and Bibron) in captivity (Hylidae, Anura, Amphibia). *Brit. J. Herp.*, **4**: 1-7.
- JONES, R. E., A. M. GERRARD, AND J. J. ROTH, 1973. Estrogen and brood pouch formation in the marsupial frog *Gastrotheca riobambae*. *J. Exp. Zool.*, **184**: 177-184.
- MATTHEWS, L. HARRISON, 1957. Viviparity in *Gastrotheca* (Amphibia: Anura) and some considerations on the evolution of viviparity. *Bull. Soc. Zool. Fr.*, **82**: 317-320.
- NIEUWKOOP, P. D., AND J. FABER, 1967. *Normal table of Xenopus laevis (Daudin)*. Second edition. North Holland Publishing Co., Amsterdam, 252 pp.
- NOBLE, G. K., 1925. The integumentary, pulmonary and cardiac modifications correlated with increased cutaneous respiration in the amphibia: a solution of the "hairy frog" problem. *J. Morphol.*, **40**: 341-416.
- NOBLE, G. K., 1927. The value of life history data in the study of the evolution of the Amphibia. *Ann. N. Y. Acad. Sci.*, **3**: 31-128.
- NOBLE, G. K., 1931. *The biology of the Amphibia*. McGraw-Hill, New York, 577 pp.
- RUGH, R., 1962. *Experimental embryology*. Burgess Publishing Co., Minneapolis, 501 pp.
- SPANNHOF, I., AND L. SPANNHOF, 1972. Beobachtungen zur Brutbiologie und Larvenentwicklung von *Gastrotheca marsupiata*. *Wiss. Z. Univ. Rostock Math.-Naturwiss. Reihe*, **20**: 97-104.
- TRUEB, L., 1974. Systematic relationships of neotropical horned frogs, genus *Hemiphractus* (Anura, Hylidae). *Occas. Pap. Mus. Natur. Hist. Univ. Kansas, Lawrence*, **29**: 1-60.
- WALKER, J., 1957. The breeding habits of the frog *Gastrotheca marsupiatum*. *Brit. J. Herp.*, **2**: 85-86.



FIGURES 42-47. *Lopezia grandiflora* subsp. *grandiflora*.—42. Flower, $\times 3.8$.—43. Near median section of flower, $\times 3.8$.—44. Capsule, $\times 3.8$.—45. Seed, adaxial view, $\times 24$.—46. Seed, abaxial view, $\times 25$. All from *Breedlove 7182* (DS).

Sepals 8-14(-15) mm long and 1.5-3 cm wide, subacute. Lower *petals* 7-13 mm long and 4-8 mm wide, upper petals 7-9 mm long and 3-4 mm wide, oblong-ob lanceolate, obtuse. *Fertile stamen* 6-8 mm long; anther 2.5-5 mm long. *Staminode* 6-8 mm, oblong-ob lanceolate. *Style* 6-7 mm long. *Capsule* 5.5-9 mm long, 4-7 mm thick. Gametic chromosome number, $n = 11$.

TYPE: Mexico, Oaxaca, Santiago el Grande, unplaced locality somewhere along the trail from Oaxaca to the Pacific Ocean, *via* Sola de Vega and Juquila, but on the Pacific slope; probably in the vicinity of Sola de Vega, whence come all other known collections. Original citation reads "Crescit in imperio mexicana prope Sant Jago el grande versus oceanum pacificum in sylvis densis, tierra templada (locis temperatis)," June–July, *C. de Karwinski* (M, herb. Zuccarini). Collected between 1827 and 1832.

Distribution (Fig. 41): Known only from the relatively open pine-oak forests N of Sola de Vega, Oaxaca, Mexico, 1500–1900 m elevation. Flowering, late August to November.

Additional specimens examined:

MEXICO. OAXACA: N of Sola de Vega, *Breedlove* 7182, 7184, 12280 (all DS), *Miranda* 3445 (MEXU), *Rzedowski* 21273 (DS, IPN, MICH, TEX).

5b. ***Lopezia grandiflora* subsp. *macrophylla*** (Benth.) Plitmann, Raven & Breedlove, *Ann. Missouri Bot. Gard.* 59: 281. 1973.

Lopezia macrophylla Benth., *Pl. Hartw.* 83, 92. 1841. Hooker, *Curt. Bot. Mag.* 79, IX: t. 4724. 1853.

Lopezia macrantha Benth. *ex* Regel, *Schweiz. Zeitschr. Gartenbau* 8: 25. 1850. (Misprint; *L. macrophylla* in the index.)

Jehlia grandiflora (Zucc.) Rose, *Contr. U. S. Natl. Herb.* 12: 297. 1909. *Miranda*, *Brittonia* 14: 46. 1962.

Jehlia macrophylla (Benth.) Rose, *Contr. U. S. Natl. Herb.* 12: 297. 1909.

Leaves 0.9–16 cm long and 0.15–6.5 cm wide, usually \pm strigose, the lower ones with 10–25 veins on each side of midrib; petioles 0.15–3 cm long. *Pedicels* 20–55 mm long, sparsely strigose to subglabrous. *Flowers* 16–26 mm long, rarely a little shorter. *Sepals* 14–23 mm long and 1.5–2.2 mm wide, angustate. Lower *petals* 15–20 mm long and 6–8.5 mm wide, subacute to obtuse at apex, elliptic-ovate to obovate; upper petals 16–21 mm long and 2.5–5 mm wide, oblong to oblong-lanceolate, subacute. *Fertile stamen* 15–18 mm long; anther 4.5–6 mm long. *Staminode* narrowly spatulate. *Style* 14–17 mm long. *Capsule* 6–11 mm long, 5–9 mm thick. Gametic chromosome number, $n = 11$.

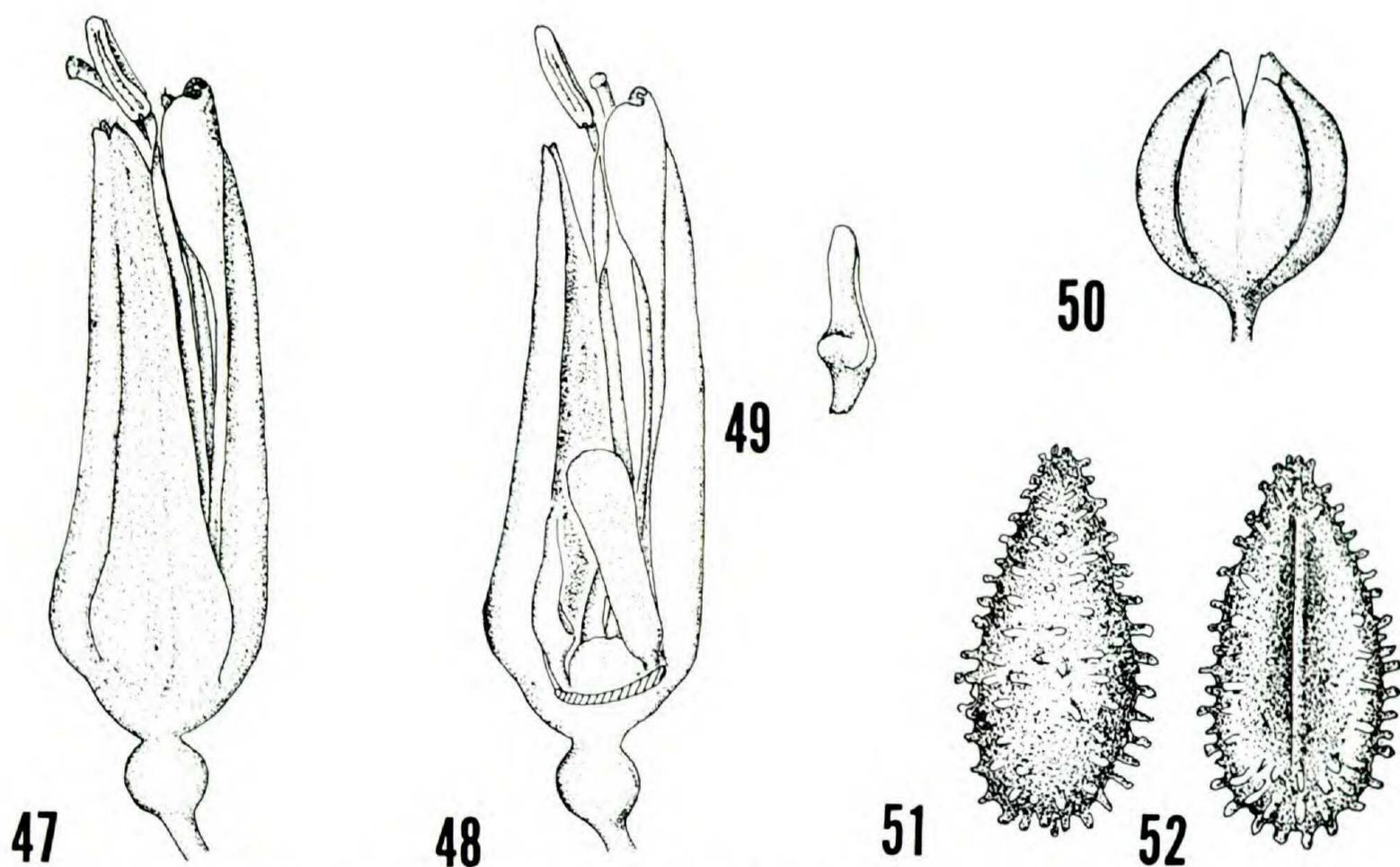
TYPE: Guatemala, Sacatepéquez, "in summo jugo inter Dueñas et Acatenango ad pedem montis ignivomi" (SW of Antigua, near the foot of the twin volcano Acatenango-Fuego), 1840, *T. Hartweg* 577 (K, lectotype, Munz, *Brittonia* 13: 79. 1961; isolectotypes, BM, G, NY, P, POM, US, W).

Distribution (Fig. 41): Pine-oak forests on the Pacific slopes of the Sierra Madre of Chiapas, Mexico, and on several of the volcanoes of north and central Guatemala, 1000–2700 m elevation. Once collected in the Sierra Madre of Oaxaca, Mexico. Flowering, late August to November.

Additional specimens examined:

MEXICO. OAXACA: 15 km S of Sola de Vega, *Rzedowski* 21299 (greatly resembling this subspecies, although collected in the area of subsp. *grandiflora*; no other specimens known from Oaxaca; DS, IPN). CHIAPAS: San Pedro Alto, *Liebmann* 3228 (GH, UC); Santa Rosa, Escuintla, *Matuda* 17848 (F); Barranca Honda, Siltepec, *Matuda* 4118 (DS, MEXU, MICH, NY); Cerro Boquerón, *Purpus* 6852 (transitional to subsp. *grandiflora*; BM, F, GH, MO, NY, UC, US); Volcán Tacaná, *Matuda* 2407 (A, F, MEXU, MICH, NY, US).

GUATEMALA. SOLOLA: Between Solola and Panajaches, *Degener* 26620 (stems and leaves hirsute, grayish-green; US). CHIMALTENANGO: Calderas, *Johnston* 1528 (F). SACATEPÉQUEZ:



FIGURES 47-52. *Lopezia langmaniae*.—47. Flower, $\times 3.5$.—48. Near median section of flower, $\times 3.5$.—49. Upper petal, $\times 3.5$.—50. Capsule, $\times 3.5$.—51. Seed, abaxial view, $\times 24$.—52. Seed, adaxial view, $\times 24$. All from *Breedlove 7161* (DS).

Volcán de Fuego, *Salvin*, 1873 (K, W); Volcán Acatenango, *Shannon & J. D. Smith 3649* (F, US). SANTA ROSA: Narango, *Heyde & Lux 3964* (G, GH, K, M, NY, POM, US). CHIQUIMULA: Cerro Brujo, *Steyermark 30964* (F); SE of Concepción de las Minas, *Steyermark 30915* (F). Without definite locality: *Heyde 348* (US), *Salvin* (K).

6. ***Lopezia langmaniae*** Miranda, *Anal. Inst. Biol. Mex.* 24: 88, *fig. 9*. 1953. Miranda, *Brittonia* 14: 46. 1962; Munz, *N. Amer. Fl. II.* 5: 17. 1965.—FIGS. 47-52.

Shrubby, \pm densely silky-hirsute *perennials*, the hairs appressed or spreading. Stems few, 5-20 dm tall. *Leaves* 0.9-20 cm long and 0.15-8 cm wide, silky-pubescent; lower leaves oblong or elliptic, attenuate or cuneate at base, acute-apiculate at apex, \pm serrulate, densely silky, with 15-24 veins on each side of midrib; upper leaves elliptic to narrowly lanceolate, subcuneate at base, acute or rarely obtuse at apex, subentire, less hairy, with 5-14 veins on each side of midrib; petioles 0.1-2 cm long and 0.1-0.25 cm wide, densely hairy. *Bracts* to 2 cm long and 1 cm wide; pedicels 14-30 mm long, \pm ascending, \pm pubescent. *Sepals* 11-17 mm long and 1-3 mm wide, 3 of them connate for 2-3 mm near the base, silky-pubescent. *Petals* whitish; lower petals 4-5.5 mm long and ca. 1.5 mm wide, linear to oblong-ob lanceolate, acute to obtuse at apex, shortly clawed; upper petals 3.5-4.5 mm long and ca. 1 mm wide, varying in size and shape, more or less linear, clawed for $\frac{1}{3}$ - $\frac{1}{2}$ of their length, subacute at apex, broad and somewhat constricted at the middle, with gland at base of limb. *Fertile stamen* 16-22 mm long; filament \pm compressed, the anther 2-3 mm long. *Staminode* 15-18 mm long, 2-3.5 mm wide, spatulate and long-clawed, retuse at apex and sometimes mucronate or rarely bearing a small reduced pale

anther, reddish. *Style* 15–21 mm long, subglabrous; stigma ca. 1 mm in diameter; ovary 1.5–2.5 mm long, 1.5–2 mm thick, pubescent. *Capsule* 4–8 mm long, 3.5–6 mm thick, subglobose to ovoid, somewhat appressed hairy-tuberculate. *Seeds* ca. 1.2–1.5 mm long, 0.6–0.8 mm thick. Gametic chromosome number, $n = 11$.

TYPE: Mexico, Chiapas, 15 km N of Tuxtla Gutiérrez near the cliffs of El Sumidero, 1200 m, 2 December 1951, *F. Miranda* 7330 (MEXU; isotypes, F, RSA).

Distribution (Fig. 41): Locally abundant on dry, rocky slopes especially in second-growth vegetation with *Tithonia*, *Dodonaea*, *Desmodium* and *Hauya*, along the eastern and northern escarpment of the central depression of Chiapas, Mexico, and northwestern Guatemala formed by the Río Grijalva, 900–1750 m elevation. Flowering, August to March.

Additional specimens examined:

MEXICO. CHIAPAS: El Sumidero, Municipio of Tuxtla Gutiérrez, *Raven & Breedlove* 19765 (leaves glabrescent), *Breedlove* 14016 (both DS); Chiapa de Corzo, *Saunders* 30 (US); Muctajoc, Municipio of Ixtapa, *Breedlove* 7289, 13782, *Laughlin* 2101, 2291, 2294 (all DS); 5 km above Soyalo, *Breedlove* 14055A (DS); Granadía, Municipio of Zinacantan, *Breedlove* 7161, 7162, 7270 (all DS); 4 mi. NW of Pinola, *Raven & Breedlove* 20112, 20115 (both DS); 3 mi. S of Aguacatenango, *Breedlove & Raven* 13128, 13456 (both DS); 1 km N of Aguacatenango, *Breedlove* 7901 (DS); without definite locality, *Ghiesbrecht* 69 (GH).

GUATEMALA. HUEHUETENANGO: Pueblo Viejo Quen Santo, *Seler* 2655 (GH).

As emphasized by Miranda (1962), *Lopezia langmaniae* is very distinct from *L. grandiflora*, even though Munz (1961) placed it in the synonymy of that species.

Section IV. *Lopezia*

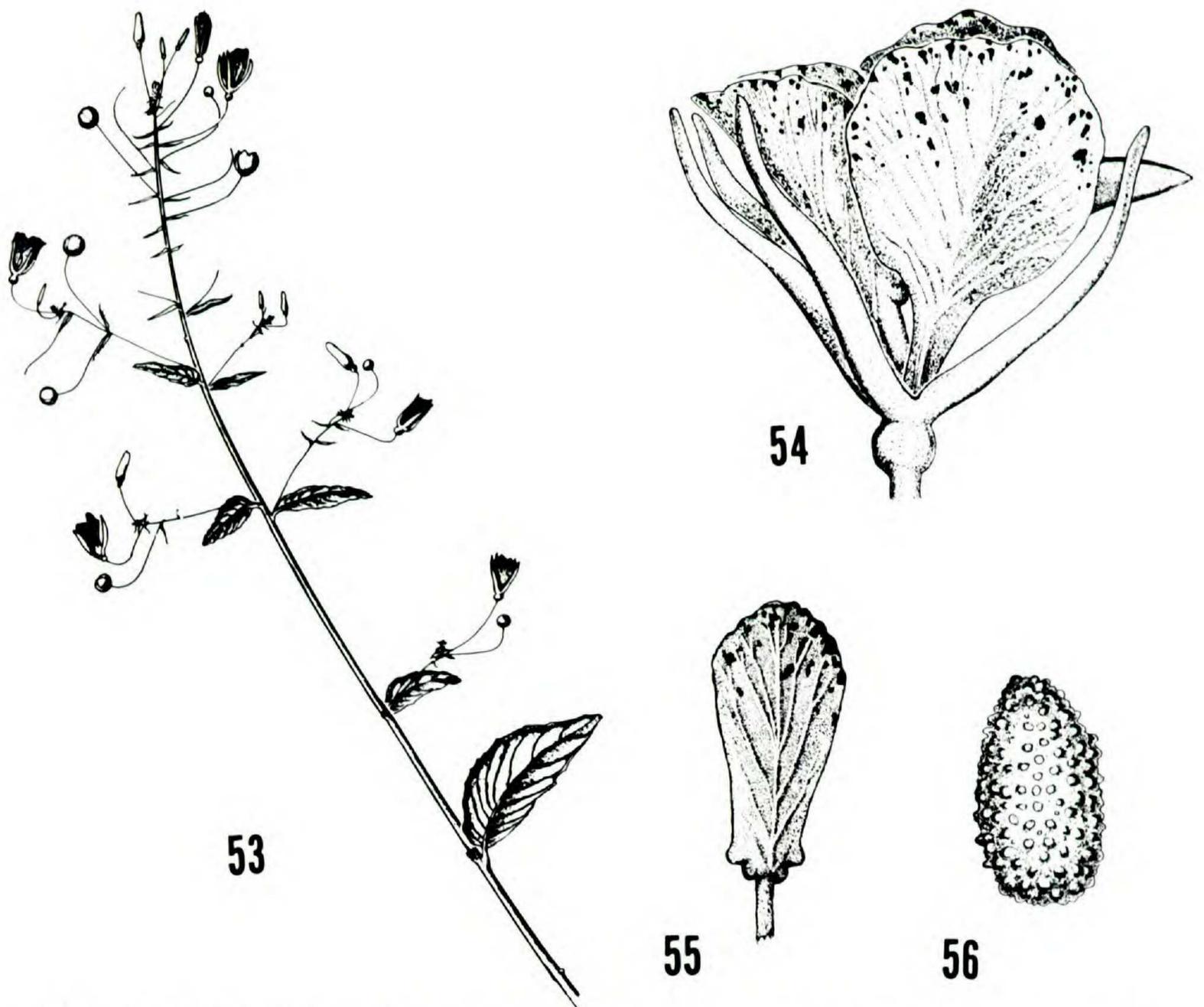
Lopezia sect. *Lopezia*

Lopezia subg. *Lopezia*; Munz, *Brittonia* 13: 77. 1961; N. Amer. Fl. II. 5: 17. 1965.

Annual or perennial *herbs*, rarely stoloniferous; two taxa with swollen underground parts; stems and inflorescences often reddish, the stems well branched, erect or ascending except in *L. racemosa* subsp. *moelchenensis*. *Leaves* alternate, rarely subopposite especially near the base or perhaps mainly opposite in *L. conjugens*. *Inflorescence* terminal, racemose or rarely paniculate, usually leafy. *Flowers* purplish or somewhat reddish to white, highly zygomorphic, markedly protandrous or autogamous, the parts free. *Sepals* subequal, divergent, often reddish. *Petals* clawed, the upper ones narrower than the lower ones, geniculate, with one or two glands (rarely 0) at the bend. *Upper stamen* fertile, the lower one petaloid, tightly clasping the fertile one and releasing it explosively upward at a touch, the staminode then reflexing sharply downward and the fertile stamen upward out of the circle of sepals while the style elongates and the stigma comes to occupy the same position as the dehiscing anther had previously; upper end of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position. *Pollen* blue. *Capsule* subglobose or obovoid, dehiscent in upper third or at apex only in *L. trichota*, often reddish. *Seeds* many, small, ± finely tuberculate. Gametic chromosome numbers, $n = 10, 9, 8, 20$.

TYPE SPECIES: *Lopezia racemosa* Cav.

Distribution: Nearly throughout Mexico and Guatemala, mainly at middle elevations, but absent from the northern deserts and lowland tropics; one species in El Salvador, Costa Rica, and Panama at middle to high elevations.



FIGURES 53-56. *Lopezia hintonii*.—53. Inflorescence, $\times 0.53$.—54. Flower, $\times 5.3$.—55. Upper petal, $\times 4.2$.—56. Seed, adaxial view, $\times 21$. All from the holotype.

Some populations occasionally lack the snapping mechanism, but it is in general the mark of a monophyletic group with closely similar flowers. *Lopezia trichota*, with its tuberous underground parts, becomes leafless in the dry season and is one of the most distinctive species. Its capsules are nearly indehiscent and probably dispersed along streams and in flash floods.

7. ***Lopezia hintonii*** Foster, Contr. Gray Herb. 155: 64. 1945.—FIGS. 53-56.

Densely hirsute *perennials*. *Stems* ca. 15 dm tall, angular, appressed-hirsute. *Leaves* 1-4 cm long and 0.2-2 cm wide, ovate to lanceolate, symmetrically or asymmetrically cuneate to obtuse at base, \pm acute at apex, remotely serrulate to subentire, appressed-hirsute, with hairy short petioles to 1 cm long. *Raceme* lax, with a few, slender branches; bracts 3-10 mm long and 0.5-2 mm wide, hairy toward tip; pedicels 11-23 mm long, ascending to spreading, glabrous. *Flowers* strongly protandrous. *Sepals* 6.5-9 mm long and 1-2 mm wide, subglabrous. Lower *petals* 7-9 mm long and 3.5-5.5 mm wide, broadly obovate, or more rarely ovate, tapering at base or shortly and broadly clawed, denticulate-sinuate to subentire at the rounded apex; upper petals 7.5-10 mm long and 2.5-4 mm wide, oblong-obovate, short-clawed with a winged claw, obsolete auricled

(subhastate), biglandular below auricles, somewhat denticulate-sinuate to entire. *Fertile stamen* 7–8 mm long; anther ca. 2 mm long. *Staminode* ca. 8–9 mm long, ca. 2 mm wide, oblanceolate, narrow at the middle, acute. *Style* distinctly shorter than stamen; stigma to 1 mm in diameter. *Capsule* to at least 3.5–5.5 mm long or longer, subglobose, glabrous. *Seeds* 1–1.5 mm long, 0.5–0.7 mm thick, oblong-ovoid, slightly incurved, finely tubercled.

TYPE: Mexico, Guerrero, Mina, Yesceros-Cruz Pacifica, rocky slope in oak forest, 2550 m, 26 November 1939, G. B. Hinton 14902 (GH; isotypes, NY, US).

Distribution (Fig. 41): Endemic in that locality. To our knowledge, no other collection has yet been made.

Unfortunately, because of the lack of recent material we have not been able to study the biology and cytology of this species. A critical feature—flower color—is unknown. Eyde and Morgan (1973) thought that it might be transitional between sect. *Jehlia* and sect. *Lopezia*, but the two glands on each upper petal seems to place it here. It seems to differ from *L. miniata* principally in its larger flowers, fruits, and seeds, and in its obscure auricles and winged claw of the upper petals.

8. ***Lopezia miniata*** Lag. ex DC., Cat. Hort. Monsp. 121. 1813. Lagasca, Gen. & Sp. Pl. Nov. 1. 1816; Munz, Brittonia 13: 80. 1961; N. Amer. Fl. II. 5: 18. 1965.

Annuals or *perennials*, sparsely to densely appressed pubescent or hirsute, with white, rusty, or reddish hairs. *Stems* 1.5–20 dm tall, pubescent or hirsute to subglabrous, subterete. *Roots* fibrous or tuberous. *Leaves* 0.7–8.5(–10) cm long and 0.15–4 cm wide, ovate or oblong-elliptic to lanceolate, obtuse, acute, or cuneate at base, acute or subacuminate at apex, serrate to subentire, hirsute, especially below, to subglabrous, sometimes with minute glandular pubescence, with (2–)4–11(–12) veins on each side of midrib; petioles (0.05–)0.1–4.5 cm long. *Inflorescence* paniculate, the terminal racemes leafy and lax or crowded; bracts 2–22 mm long and 0.5–6 mm wide; pedicels 5–35 mm long, spreading to more or less ascending-rarely suberect, puberulent, glandular-strigulose, or subglabrous. *Flowers* strongly protandrous. *Sepals* 3.5–7 mm long and ca. 1 mm wide, glabrous or with a few hairs near apex and rarely also at base. *Petals* white, pinkish, orange, or lilac; lower petals 4.5–9(–10) mm long and 1.5–5 mm wide, linear to suborbicular, long-clawed, subacute or obtuse, entire to crenulate at the apex; upper petals 4–8 mm long and 0.8–2 mm wide, linear to narrowly spatulate, the limb distinctly biauriculate near the base, with two pink or red glands below the auricles, entire, dentate, or crenulate at the apex. *Fertile stamen* 3.5–5.5 mm long; anther 1–2 mm long, gray to brownish. *Staminode* 3.5–5 mm long and 1.5–3 mm wide, obovate-spatulate, ± emarginate at apex, same color as the petals. *Style* 3–5 mm long; stigma 0.3–0.6(–0.7) mm in diameter, white or pink; ovary 1–1.5 mm thick, subglobose, subglabrous or sparsely pubescent near apex. *Capsule* 1.5–4.5(–5) mm long, 1.5–4(–5) mm thick, subglobose, subglabrous. *Seeds* 0.6–1.2 mm long, 0.5–0.6 mm thick, ovoid, finely tuberculate, brown. Gametic chromosome number, $n = 10$.

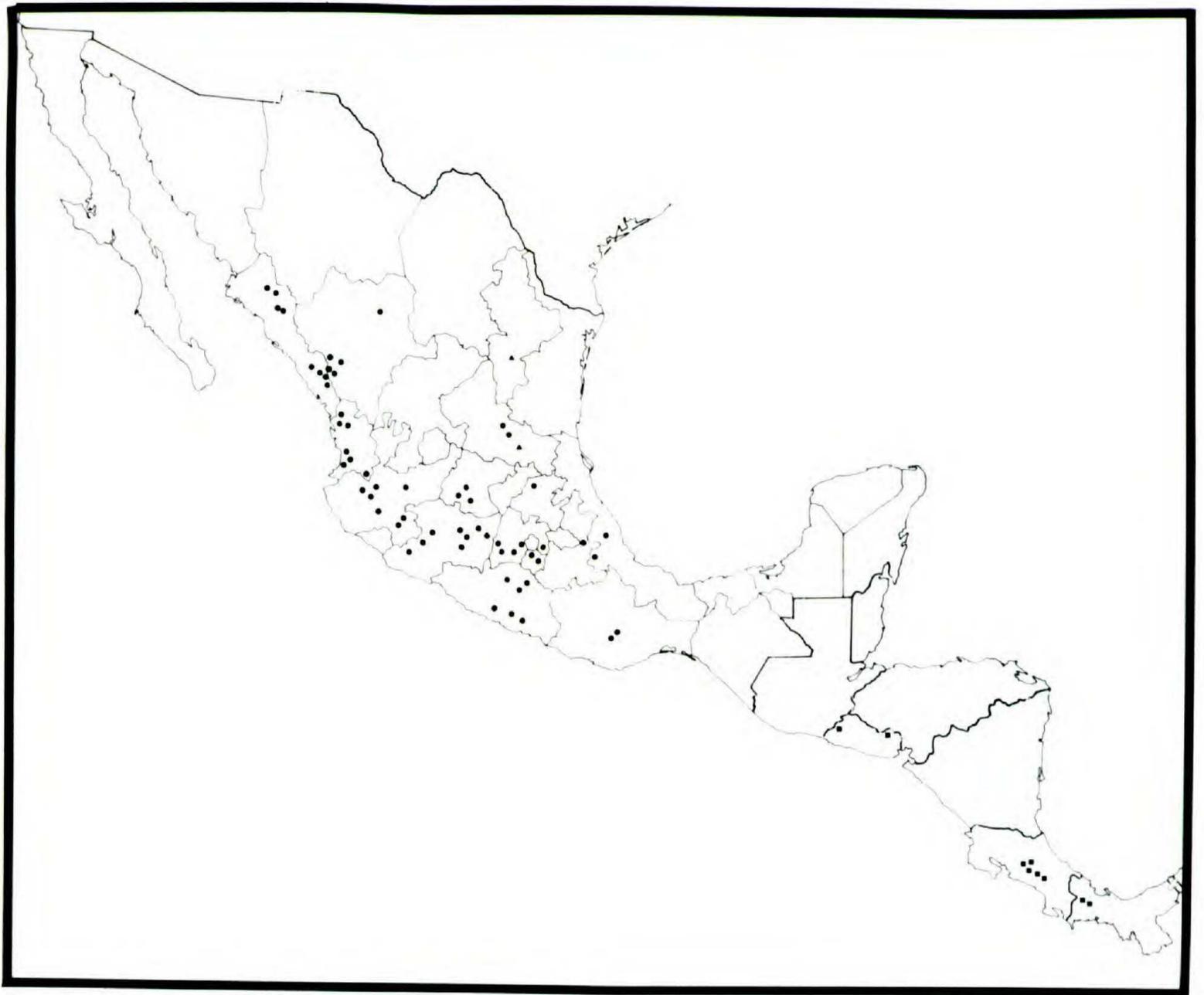


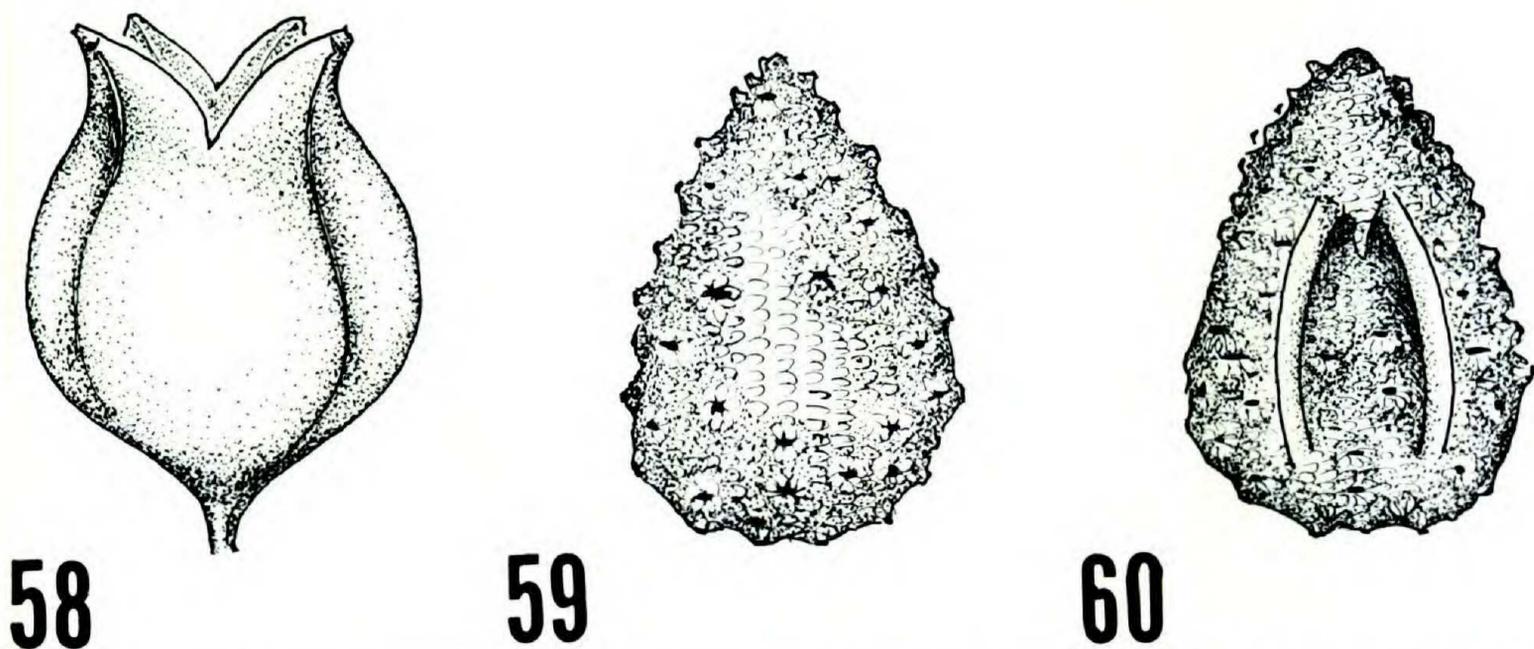
FIGURE 57. Geographic distribution of *Lopezia miniata* subsp. *miniata* (dots), *L. miniata* subsp. *paniculata* (squares), and *L. nuevo-leonis* (triangles).

Distribution (Fig. 57): Shrubby or open situations at middle elevations, often weedy, from northern Sinaloa and Durango in the Sierra Madre Occidental south to Veracruz, Mexico; El Salvador, Costa Rica, and Panama, 700–3000 m elevation. Flowering, (August–) November to March.

The southern disjunct populations of this species have generally been regarded as a distinct species, *Lopezia paniculata* Seemann. They differ chiefly in their more crowded inflorescences and tuberous underground parts. In the experimental garden, northern and southern populations could be intercrossed without difficulty, producing fertile hybrids. The relationships between the northern populations of this species and the less variable southern ones can best be understood and demonstrated in the context of the genus, we believe, by regarding them as subspecies of a single species.

KEY TO THE SUBSPECIES

- Roots fibrous; leaves and lower petals partly denticulate; racemes lax; Mexico 8a. subsp. *miniata*
 Roots usually tuberous; leaves and lower petals subentire; racemes usually crowded; El Salvador, Costa Rica, and Panama 8a. subsp. *paniculata*



FIGURES 58–60. *Lopezia miniata* subsp. *miniata*.—58. Capsule, $\times 11$.—59. Seed, abaxial view, $\times 36$.—60. Seed, adaxial view, $\times 36$.

8a. *Lopezia miniata* subsp. *miniata*.—FIGS. 58–60.

Lopezia frutescens Roem. & Schult., Syst. 1: 34. 1817. Type: BM, herb. Roemer, "habit in Mexico"; cultivated (?) in W.

Lopezia pumila Bonpl., Desc. Jard. Malm. 1813: 67. 1815. Type: Mexico, Guanajuato, near Guanajuato, A. Bonpland (P, herb. Bonpland, lectotype).

Lopezia fruticosa Hort. Par. ex Schrank, Nov. Act. Nat. Cur. 9: 91. 1818, and Pl. Rar. Hort. Acad. Monac. 1: fol.20. 1818/19. Type: Portenphlag Herbarium and cultivated in W probably from the authentic material; Hort. bot. Monac., herb. Zuccarini, "*L. fruticosa* Schrank, h. in Mexico" 1820 (M, cultivated from the authentic?).

Lopezia pubescens HBK., Nov. Gen. & Sp. 6: 96. 1823. Type: Mexico, Michoacán, Patzcuaro, 6780 ft., A. von Humboldt & A. Bonpland (P).

Lopezia oaxacana Rose, Contr. U. S. Natl. Herb. 12: 229, fig. 42. 1909. Type: Mexico, Oaxaca, San Felipe, 10 October 1897, C. Conzatti & V. González 509 (US 574,851; isotype, GH).

Lopezia palmeri Rose, Contr. U. S. Natl. Herb. 12: 299, fig. 43. 1909. Type: Mexico, Durango, San Ramón, 21 April–18 May 1906, E. Palmer 85 (US 571,100; isotypes, GH, K, MO, NY, S, UC).

Lopezia violacea Rose, Contr. U. S. Natl. Herb. 12: 301, fig. 48. 1909. Type: Mexico, Morelos, Sierra de Tepoxtlán, 2350 m, 30 October 1900, C. G. Pringle 8358 (US 381,869; isotypes, BM, DS, G, GH, MEXU, MO, NY, POM, UC, W, Z).

Lopezia stricta Rose, Contr. U. S. Natl. Herb. 12: 301, fig. 47. 1909. Type: Mexico, Jalisco, Sierra Madre W of Bolaños, 15–17 September 1897, J. N. Rose 2979 (US 301,735; isotypes, GH, NY).

Lopezia pauciflora Sprague & Riley, Jour. Bot. 62: 15. 1924. Type: Mexico, Sierra Madre Occidental, B. C. Seemann 2169 partim (K).

Lopezia tepicana Sprague & Riley, Jour. Bot. 62: 15. 1924. Type: Mexico, Nayarit, Tepic, Sinclair (K).

Lopezia globosa M. E. Jones, Contr. West. Bot. 15: 147. 1929. Type: Mexico, Nayarit, Tepic, M. E. Jones 23299 (POM).

Annuals or perennials, sparsely to densely appressed-pubescent or hirsute, with white, rusty, or reddish hairs. Leaves serrate to subentire. Inflorescence leafy and rather lax. Petals white, pinkish, orange, or lilac; lower petals (4.5–) 4–9(–10) mm long and 2–5 mm wide, denticulate or crenulate to subentire at the apex; upper petals 5–8 mm long and 0.8–2 mm wide. Seeds 0.6–1(–1.2) mm long. Gametic chromosome number, $n = 10$.

TYPE: Cultivated at Montpellier, France, the seeds sent from Mexico by Martin Sessé y Lacasta, 1804, *A. P. De Candolle* (G-DC; probable isotype, US). Possibly the same material used for the illustration of *Enthomanthus fibrosus* by Mociño and Sessé.

Distribution (Fig. 57): Mexico, almost ubiquitous in pine-oak vegetation but also very common as a roadside weed and as a weed in *milpas* from northern Sinaloa and Durango, south through the Sierra Madre Occidental to central Oaxaca and across the Tarns-Mexican Volcanic Belt to Veracruz with a few scattered localities in Hidalgo and San Luis Potosí, 700–3000 m elevation. Flowering, (August–) November to March.

Representative specimens examined:

MEXICO. SINALOA: Balboa, San Ignacio, *Ortega* 1152 (DS, MEXU); Cerro de la Silla, San Ignacio, *Móntez & Salazar* 734 (US); Santa Lucía, Concordia, *Ortega* 6035 (IPN); 19 mi. E of Concordia on Mex. Hwy. 40, *Breedlove* 1621 (DS, RSA); 45 mi. E of Concordia, *Breedlove* 4249 (DS); Capadero, Sierra Tacuichamoma, *Gentry* 5536 (DS, GH, MEXU, MICH, MO, NY, UC, US); Ocurahui, Sierra Surutato, *Gentry* 6423 (MICH); Canon Tarahumare at La Joya, Sierra Surutato, *Breedlove* 15608 (DS); 4 mi. W of Surutato, Sierra Surutato, *Breedlove* 15598 (DS). DURANGO: La Bajada, Tamazula, *Ortega* 595 (DS, IPN, MEXU), 4265 (US); Sianori, *Ortega* 5361 (US, K); Sierra Tres Picos, *Gentry* 5297 (DS, GH, MEXU, MICH, MO, NY, UC, US); 19 mi. SW of San Ramón, *Palmer* 85; 13 mi. W of La Ciudad, *Breedlove* 15549 (DS); 9.3 mi. E of El Palmito, Pueblo Nuevo, *Breedlove* 4256 (DS). NAYARIT: Tepic, *Palmer* 1893 (DS, GH, MICH, S, UC, US), *Jones* 23189 (POM); N of Compóstela, *McVaugh & Koelz* 513 (MEXU, MICH, RSA, US); vicinity of Jalisco, *Ferris* 5825 (A, DS, US); 10 mi. SE of Ahuacatlán, road to Barranca del Oro and Amatlán, *McVaugh & Koelz* 802 (MICH); W side of Cerro de Sanganguéy, *Breedlove* 8053, *Breedlove & Gregory* 14218 (both DS). SAN LUIS POTOSÍ: "Sanguedo," *Schaffner* 640 (GH, K; NY, pro parte); Sierra de Álvarez, around Puerto Huerta, Zaragoza, *Rzedowski* 4184 (IPN); Cerro Grande, NW of Guadalcazar, *Rzedowski* 5067 (RSA); exact locality not known, *Schaffner* 443 (BM, G, MICH, NY, P, UC). GUANAJUATO: Ravín de "la Esperanza," 6 km from Guanajuato, 1893, *Dugés* (GH); León, *Rose & Rose* 11508 (NY, US); Ojo de Agua, S of Abásolo, *Sohns* 243 (US). HIDALGO: 20 km NE of Zimapan, *González Quintero*, 1965 (with a few features of *L. racemosa*, e.g. scarcely auricled petals; DS). JALISCO: Sierra de Manantlán, SE of Autlán, *McVaugh* 23099 (hairy form with large petals; IPN, MICH), *Hooper*, 1953 (MICH); La Barranca, Guadalajara, *Jones* 27077 (a delicate many-stemmed form with lilac narrow petals; BM, DS, MICH, MO, NY, RSA, UC, US); Sierra de la Campana, W of Los Volcanes, *McVaugh* 20026 (MICH); Etzatlán road to San Domingo mines, *Barnes & Land* 298 (K, US), *Rose & Painter* 7514 (US), *Pringle* 11454 (DS, GH, MEXU, MICH, MO, UC, US); Sierra del Tigre, S of Mazamitla, *McVaugh & Koelz* 427 (MICH, RSA); Sierra del Halo, *McVaugh & Koelz* 1251 (MICH); Sierra de Cuale, SW of Talpa de Allende, *McVaugh* 14377 (MEXU, MICH, RSA, US), 14259 (MEXU, MICH, RSA); 12 mi. W of Autlán on Mex. Hwy. 80, *Breedlove* 8069 (DS); 11 mi. W of Tecalitlán, on Mex. Hwy. 110, *Breedlove* 8072 (DS); Barranca W of Atenquique, Tuxpán, *Rzedowski* 21934 (IPN). MICHOACÁN: Near San Lorenzo, N of Uruapán, *Frye & Frye* 3056 (DS, GH, POM, UC); 3 km S of Tacambaro, on road to Pedernales, *Rzedowski* 23724 (DS, IPN); ca. 17 mi. E of Morelia, *Breedlove* 7228A (DS); 5 mi. S of Zinapécuaro, *Breedlove* 7217 (DS); Morelia, Cerro Azul, *Arsène* 2830 (BM, K, MO, NY, US); Sierra Torrecillas, Coalcomán, *Hinton et al.* 12337 (G, GH, K, MICH, NY, P, S, UC, US, W), 15264 (US 1,977,671; sheets in other herbaria are *L. racemosa*); Patzcuaro, *Pringle* 3953 (BM, DS, G, GH, IPN, K, M, MEXU, MO, NY, P, POM, S, UC, US, W, Z); W of Jacona, *Ripley & Barneby* 14067 (NY). GUERRERO: Pie de la Cuesta Toro Muerto, dist. Galeana, *Hinton* 11075 (unique tall form with large flowers, leaves and panicles; G, GH, K, M, MICH, MO, NY, S, UC, US, W); Sierra Madre del Sur, N of Río Balsas, *Mexia* 8786 (G, GH, MO, NY, RSA, S, UC, US); Plan del Carrizo, *Hinton et al.* 11026 (GH, K, MICH, NY, UC, US); above Los Ranchos, W of Teloloapán, *Porter* 1357 (DS, GH, MEXU); 2 mi. NW of Filo del Caballo, *Breedlove* 15826 (DS); 2 mi. E of Omiltemi, *Breedlove* 15817 (DS); Mountains SW of Taxco, *Ripley & Barneby* 13725 (DS). MEXICO: Tultenango, *Rose & Painter* 7824 (GH, NY, US); Rincón, Temascaltepec, *Hinton et al.* 6792 (G, GH, K, MICH, NY, S, UC, US, W), *Hinton* 209 (MEXU); Tejupilco, Temascaltepec, *Hinton et al.* 7327 (GH,

K, NY, US); Ozumba, *Pringle* 8713 (BM, G, GH, IPN, K, M, MEXU, MICH, NY, P, RSA, TEX, UC, US, W), 9797 (GH, MO, NY, US, Z); Cerro Ajusco, *Mexia*, 1922 (UC); Jilotepec, *Matuda et al.* 26724 (MEXU); Valle Bravo-Ixtapantango, *Miranda* 4797 (MEXU); 15 mi. E of Zitacuaro on Mex. Hwy. 15, *Breedlove* 8074 (DS); Coatepec Harinas, *Ripley & Barneby* 13759 (DS). MORELOS: Casa del Tepozteco, *Seler* 4328 (GH); Sierra de Tepoxtlán, *Pringle* 8357 *p.p.* (G, IPN, MEXU, NY, US, Z); S of the village of Tepoztlán, *Ripley & Barneby* 14549 (DS); Amatlán, *Miranda* 918 (MEXU); 3 mi. S of Tres Cumbres, *Breedlove & Gregory* 14232 (DS). PUEBLA: Cerro Sta. Maria de Zacatepec, *Arsène* 3511 (MO, NY, P, US). VERACRUZ: Near El Puerto, above Acultzingo, *Sharp* 44659 (RSA); near Jalapa, *Pringle* 9230 (TEX, UC). OAXACA: Sierra de San Felipe, *Ch. L. Smith* 844 *p.p.* (leaves, flowers and capsules larger than usual; MO, US); Santa Cruz, Orillas del San Antonio, *Conzatti et al.* 4097 (US); Oaxaca, *Conzatti & Gonzales* 1055 *p.p.* (GH), *Ghiesbreght* 261? (P); Las Sedas, *Conzatti* 2030 (BM, MEXU).

Lopezia miniata subsp. *miniata* is highly variable and polymorphic. Its variation is parallel to that of *L. racemosa* subsp. *racemosa* (e.g. in color of petals). Both taxa are widely distributed in Mexico, growing sympatrically in many localities and occupying almost the same habitats. In spite of the overall similarity between the two, a detailed examination shows that *L. miniata* subsp. *miniata* is well defined by an assemblage of characters: leaves never distinctly serrate; petals never oblong; claws of petals never ciliolate; lower petals denticulate or subentire, upper petals truncate-obtuse to usually slightly retuse or few-denticulate, distinctly biauriculate and with 2 obvious glands; stigma minute; capsules small. It flowers mainly in the dry season (November–March) whereas *L. racemosa* flowers mainly in the wet season (June–October).

The variability of *Lopezia miniata* subsp. *miniata* is particularly pronounced in:

1. *Habit*: Perennials *vs.* annuals, the latter sometimes differing considerably from the more common perennials; the perennials flower in their first year. Unusual forms are more common among the annuals. Stems may be few or many, simple (e.g. "*L. pumila*") or branched, short or very long, ascending, erect, or decumbent.

2. *Pubescence*: From densely hirsute or pubescent (e.g. "*L. pubescens*") to subglabrous. The variation occurs between and within populations as well as on individual plants. The hairs may be of different kinds and positions, spreading to usually appressed, and in different proportions. The various parts are almost independently variable in this character, though hairy bracts and buds have not been found in glabrescent plants. Only hairy specimens have been recorded from the east (Hidalgo, Puebla, Veracruz).

3. *Leaf*: Wide range of variation in dimensions and general morphology. Of all organs the leaves show the most age- and season-related variability.

4. *Petals*: Variable in size (e.g. *Espinosa* 103 from Morelos with small flowers *vs.* *Hinton* 5343 from Mexico with long petals) and color. Two divergent types have been observed: Corolla with the dominant color white, tinged with pink, lilac, blue or even violet (e.g. "*L. violacea*") as distinct from corolla pink-reddish or orange to red. The first form has usually smaller capsules and flowers, upper petals truncate to retuse-denticulate and lower petals denticulate; the second form is sometimes long-stemmed, with larger flowers, particularly petals, usually with bigger capsules, the upper petals somewhat retuse and the lower \pm retuse but subentire. The "whitish-flowered" type is distributed mainly in the

north (Sinaloa, Durango, Nayarit south to México) and very scattered in the south (Guerrero); the "reddish-flowered" type occurs mainly in south and central Mexico, from Nayarit and San Luis Potosí to Oaxaca. The "whitish-flowered" type is better represented in herbaria, probably because more specimens have been collected in northern Mexico. Nevertheless, it seems that the "reddish-flowered" form is as common as the other one and more widespread; it is less weedy, growing chiefly in primary habitats. We did not keep these two forms apart, as distinct subspecies, for several reasons: they are easily crossed; the morphological differences are not clear-cut as all characters show a \pm continuous variation, except for the color which in itself is not considered a useful character upon which to delimit subspecies; they are not separate eco-geographically.

5. *Glands and auricles*: The glands are variable in size, color and position, but the range of variation is rather narrow. They may be close together or apart, equal or rarely one smaller. More variable are the auricles which can be short or long, wide or usually narrow, spreading straight to bent upwards.

6. *Capsules*: Generally smaller than those of *L. racemosa* but sometimes to 5 mm in diameter. There is also some variation in the number of fruits (or flowers, e.g. "*L. pauciflora*") per plant, though commonly the inflorescence is many-branched and many-fruited.

The various mentioned characters are uncorrelated (e.g. pubescent plants may have whitish or reddish flowers, smaller or larger capsules, and are not restricted to certain localities). For this reason the species has a complex synonymy. It is preferable to treat this taxon as one polymorphic entity, following Munz (1961), instead of recognizing in it a multitude of ill-defined subdivisions.

A few extreme forms of *Lopezia miniata* should be noted explicitly:

a). Plants with short, nodding and bowed pedicels; flowers small; upper petals with short but broad auricles and 2 adjacent glands; capsule wide (\pm 3.5 mm). Mexico, Michoacán: Cerro Azul, near Morelia, 4 November 1909, *Arsène* (NY). This is so far one of the very few plants collected which share a few features with *L. racemosa* (others are *Conzatti & Gonzalez 509* from Oaxaca and *González Q.*, 1965, from Hidalgo). No other natural hybrids or transitions between the two species have been found, though in many respects (stature, pubescence, dimensions of flowers and capsules) they show homologous, almost parallel, variability. This phenomenon accounts for many misidentifications of both, especially in herbarium material.

b). Plants with long stems and large leaves; flowers and capsules larger than usual; glands minute; but (sepals) with few long hairs at base and tip. Mexico, Oaxaca, San Felipe, 10 October 1897, *Conzatti & González 509* (GH, US; type collection of *L. oaxacana* Rose); Sierra de San Felipe, 2 October 1894, *C. L. Smith 844 pro parte* (MO, US; paratypes of *L. oaxacana*).

c). Plants with long stems, glabrescent; leaves large (to 9 cm long and 5 cm wide); racemes \pm paniculate; ovary and bud long-ciliate. Mexico, Veracruz near El Puerto, above Acutzingo, 6 September 1944, *Sharp 44659* (RSA).

d). Plants with hirsute and hispid-pubescent stems; some leaves subopposite; pedicels glandular-puberulent to pubescent; petals large, the upper ones oblanceolate to oblong; fertile stamen long (5–6 mm). Mexico, Jalisco, Sierra de

Manantlán, SE of Autlán, between El Chante and Cuzalapa, 19–22 March 1965, R. McVaugh 23099 (IPN, MICH).

e). Tall (to 3 m²), pubescent plants; leaves long (to 11 cm), the upper sub-opposite; inflorescence long, branched, many-panicled; stipules acicular-subulate; bracts and buds \pm hirsute; all floral parts longer than usual; corolla orange; capsule 0.3–0.55 mm; seeds ca. 1.1 mm long, brown-red. Mexico, Guerrero, Dist. Galeana, Pie de la Cuesta Toro Muerto, 17 December 1937, G. B. Hinton 11075 (G, GH, K, MICH, MO, NY, S, UC, US, W). Probably an undescribed taxon, related to *L. miniata* but quantitatively distinguished. This collection seems to approach the type of *L. hintonii* in its characteristics.

f). Delicate plants with many thin stems, hirsute-pubescent to glabrescent; leaves narrower than usual, subentire; inflorescence paniculate, many flowered; pedicels slender, glandular-puberulent; flowers (in herb.) lilac-violet; petals narrow, long clawed; seeds finely tubercled. Mexico, Jalisco, Guadalajara, La Barranca, 17 November 1930, M. E. Jones 27077 (BM, DS, MICH, MO, NY, RSA, UC, US). Probably an undescribed taxon, closely related to *L. miniata*.

8b. *Lopezia miniata* subsp. *paniculata* (Seemann) Plitmann, Raven & Breedlove, comb. nov.

Lopezia paniculata Seemann, Bot. Voy. Herald 120. 1853. Munz, Brittonia 13: 82. 1961; N. Amer. Fl. II. 5: 19. 1965.

Densely hirsute *perennials*. *Leaves* remotely serrulate to subentire. *Inflorescence* usually of short and crowded terminal racemes. *Petals* white or reddish-pink; lower petals 5–7 mm long and 1.5–3 mm wide, somewhat retuse or subentire at the apex; upper petals 4–7 mm long, ca. 1 mm wide. *Seeds* ca. 1.2 mm long. Gametic chromosome number, $n = 10$.

TYPE: Panama, Boquete, March 1848, B. C. Seemann 1225 (K; isotype, BM).

Distribution: Moist or dry places such as slopes, canyons and even roadsides, in shrubby or open formations in El Salvador, Costa Rica and Panama, (850–)950–2000(–2600) m elevation. Flowering mainly from November to March, but sporadically throughout the year.

Representative specimens examined:

EL SALVADOR. MORAZON: Montes de Cacaquatique, Tucker 663 (MICH, RSA, UC, US). AHUACHAPAN: Apaneca, Pittier 2010 (racemes rather long, upper leaves and bracts subglabrous; US).

COSTA RICA. ALAJUELA: Cerros de San Rafael de San Ramón, Brenes 5905 (CR, NY), 5923a (CR), 21999 (NY). SAN JOSÉ: Cerro de Piedra Blanca, above Escasú, Standley 32555, 35776, 41381 (all US); Paraíso, J. D. Smith 6503 (US); Río Blanco, NE of El Copey, Standley 41909 (US). CARTAGO: San Cristóbal de Candelaria, Pittier 3679 (NY, US); Cerro de la Carpintera, Standley 34210 (US); Volcán de Irazú, Holway 282 (POM, US).

PANAMA. CHIRIQUÍ: El Boquete, Killip 3505 (US), Pittier 2890 (NY, US); Cerro Punta near El Volcán, Río Chiriquí Viejo valley, G. White 30 (GH, MO); Volcán de Chiriquí Viejo, Allen 987 (G, GH, MO, US); Bajo Mono, district Boquete, Davidson 493 (MO, US).

Lopezia miniata subsp. *paniculata* is variable in stature (height), pubescence, dimensions of leaves and racemes, and to a lesser extent in flower-color, length of raceme and size of capsule. Nevertheless, it is much less variable than the northern, widespread subsp. *miniata*, from which it has almost certainly been

derived. Plants of subsp. *paniculata* with elongated, loose and leafy racemes have been collected occasionally (*Davidson* 493 from Panama; *Pittier* 2010 from El Salvador; *J. León* 2207 and *Smith* 6503 from Costa Rica). It is not certain how constant the tuberous underground parts may be in this subspecies, as they are rather infrequently collected.

9. ***Lopezia suffrutescens*** Munz, *Brittonia* 13: 80. 1961. Munz, *N. Amer. Fl.* II. 5: 18. 1965.—FIGS. 61–62.

Robust, bushy, subglabrous, fleshy *perennials*. *Stems* 4–8 dm tall, thick, juicy, well branched; branches \pm angular, subglabrous but sparsely hirtellous near the inflorescence. *Leaves* 1–7.3 cm long and 0.3–4 cm wide, thick and \pm fleshy, ovate or lanceolate, obtuse and sometimes asymmetrical at base, acute or acuminate at apex, acutely serrate or serrulate, with 3–9 veins on each side of midrib, ciliolate along margins and veins; petioles 0.15–2.5 cm long, narrowly winged, sparsely hispidulous. *Bracts* 5–42 mm long, 1.5–11 mm wide, glabrous; pedicels ascending to recurved-spreading, to 3.5 cm long. *Flowers* strongly protandrous, evidently nectariferous. *Sepals* 6–14 mm long and 1–2 mm wide, subglabrous but with a few erect hairs near tip and base. *Petals* pale pink or white; lower petals (7–)8–14 mm long and (3–)5–9.5 mm wide, obovate or spatulate to subdeltoid, tapering into a long claw, rounded and subentire or somewhat crenulate at apex; upper petals more deeply lined with pink, (7–)8–14 mm long and 2–7 mm wide, spatulate or oblong-oblancheolate, obtuse and subentire or somewhat crenulate at apex, narrowed then broadly auriculate at base, the auricles 1–2.2 mm high, subtended by 2 green glands on each petal, the petals subsessile. *Fertile stamen* 6–11 mm long, reddish. *Staminode* 5–10 mm long and 2.5–4 mm wide, petaloid, obovate-spatulate and \pm emarginate to obcordate, white or pale pink. *Style* 6–12 mm long, pale pink; stigma 0.6–1 mm in diameter; ovary subglobose, glabrous. *Capsule* 3–5 mm thick, subglobose, glabrous. *Seeds* 1–1.5 mm long, 0.3–0.5 mm thick, oblong-ovoid, tuberculate, dark brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Durango, La Bajada, Tamazula, 1921, *J. G. Ortega* 4264 (US; isotypes, IPN, MEXU, POM, US), 567 (MEXU, probably part of the type collection).

Distribution (Fig. 41): Known only from two steep-walled canyons in Sinaloa and Durango, Mexico, 1200–1500 m elevation. Flowering February and March. *Lopezia ciliatula* is restricted to the same two areas, as far as known.

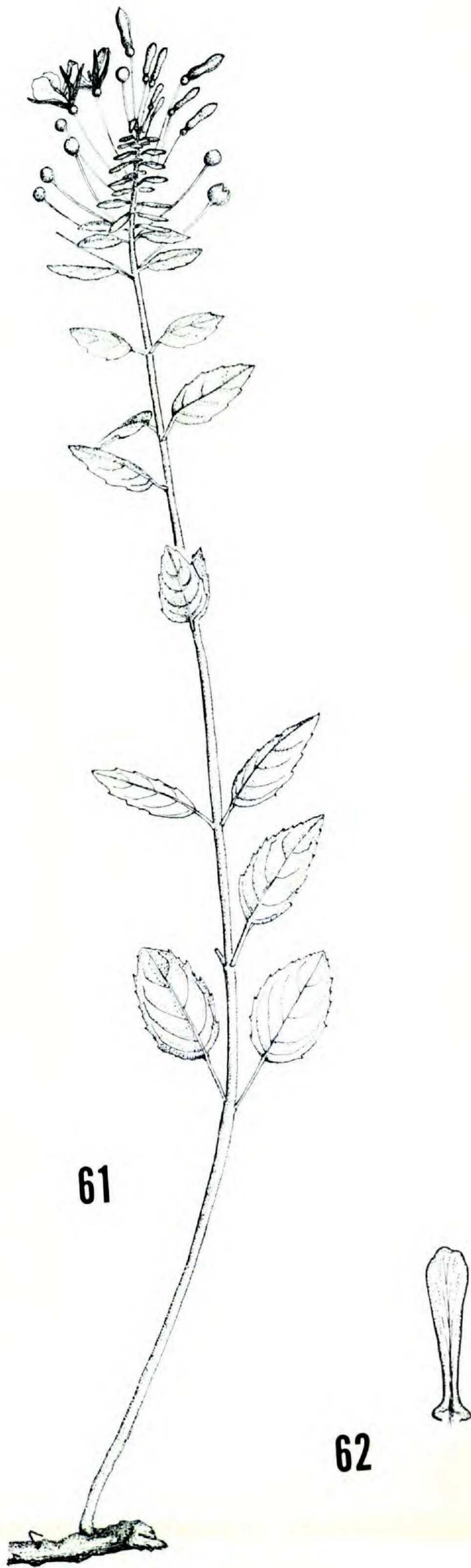
Additional specimens examined:

MEXICO. SINALOA: Cañon de Tarahumare, Sierra Surutato, *Gentry* 7302 (GH, MICH, NY). DURANGO: Río Tamazula between La Bajada and La Junta, ca. 1500 m, *Breedlove* 24534 (CAS).

As Munz (1961: 88) pointed out, *Lopezia suffrutescens* is amply distinct among the bituberculate species. It is very attractive, with its large pale flowers.

→

FIGURES 61–62. *Lopezia suffrutescens*.—61. Branch, \times 0.6.—62. Upper petal, \times 2.4. Both from the holotype.



Judging from its reduced chromosome number, $n = 9$, it was probably derived from large-flowered ancestors with $n = 10$, perhaps resembling *L. hintonii* or the population of *L. miniata* from Guerrero described on p. 523.

10. ***Lopezia nuevo-leonis*** Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 280. 1973.—FIGS. 63–65.

Sparsely strigulose to glabrous *annuals* or *perennials*. *Stems* 2.5–7 dm tall, angular. *Leaves* 0.6–4 cm long and 0.2–2.5 cm wide, oblong-ovate to lanceolate, rounded to broadly cuneate at base, subacute or acuminate at apex, acutely serrate, \pm fleshy, subglabrous, with 2–6 veins on each side of midrib; petioles 0.1–3.8 cm long, scarcely strigulose or glabrous. *Bracts* 3–13 mm long and 1–4 mm wide, subglabrous; pedicels 8–21 mm long, ascending, appressed and shortly pubescent on one side, subglabrous on the other. *Flowers* mainly autogamous. *Sepals* 4.5–7 mm long and 1 mm wide, glabrous. *Petals* pink and reddish; lower petals 5–8 mm long and 2–3.5 mm wide, obovate, somewhat asymmetrically angustate into a long claw, rounded at apex, sometimes subcrenulate or slightly retuse; upper petals 5–8.5 mm long and 1–1.5 mm wide, narrowly oblanceolate, \pm obtuse, clawed, shortly and obtusely auricled with 2 adjacent pink glands on each one. *Fertile stamen* 4–5 mm long; anther 1.5–2 mm long, bluish-gray. *Staminode* 3.5–4.5 mm long and 2–3 mm wide, broadly obovate, ultimately shedding pollen directly on the stigma, abruptly clawed, emarginate at apex, pink-reddish but whiter below. *Style* 3–4 mm long; stigma 0.5–1.1 mm in diameter; ovary mostly glabrous but shortly pubescent below, subglobose. *Capsule* 3–5 mm long, 2–4 mm thick, oblong or ovoid-ellipsoid, subglabrous. *Seeds* 0.9–1.1 mm long, 0.6–0.8 mm thick, oblong-ovoid, slightly incurved, coarsely rugose-tubercled, blackish. Gametic chromosome number, $n = 8$.

TYPE: Mexico, Nuevo León, Sierra Madre Oriental, Santa Rosa Canyon, 21 mi. W of Linares, cool N-facing talus and rock ledges, 2100 ft. elevation, 28 October 1964, *H. D. Ripley & R. C. Barneby 13569* (DS; isotype, NY).

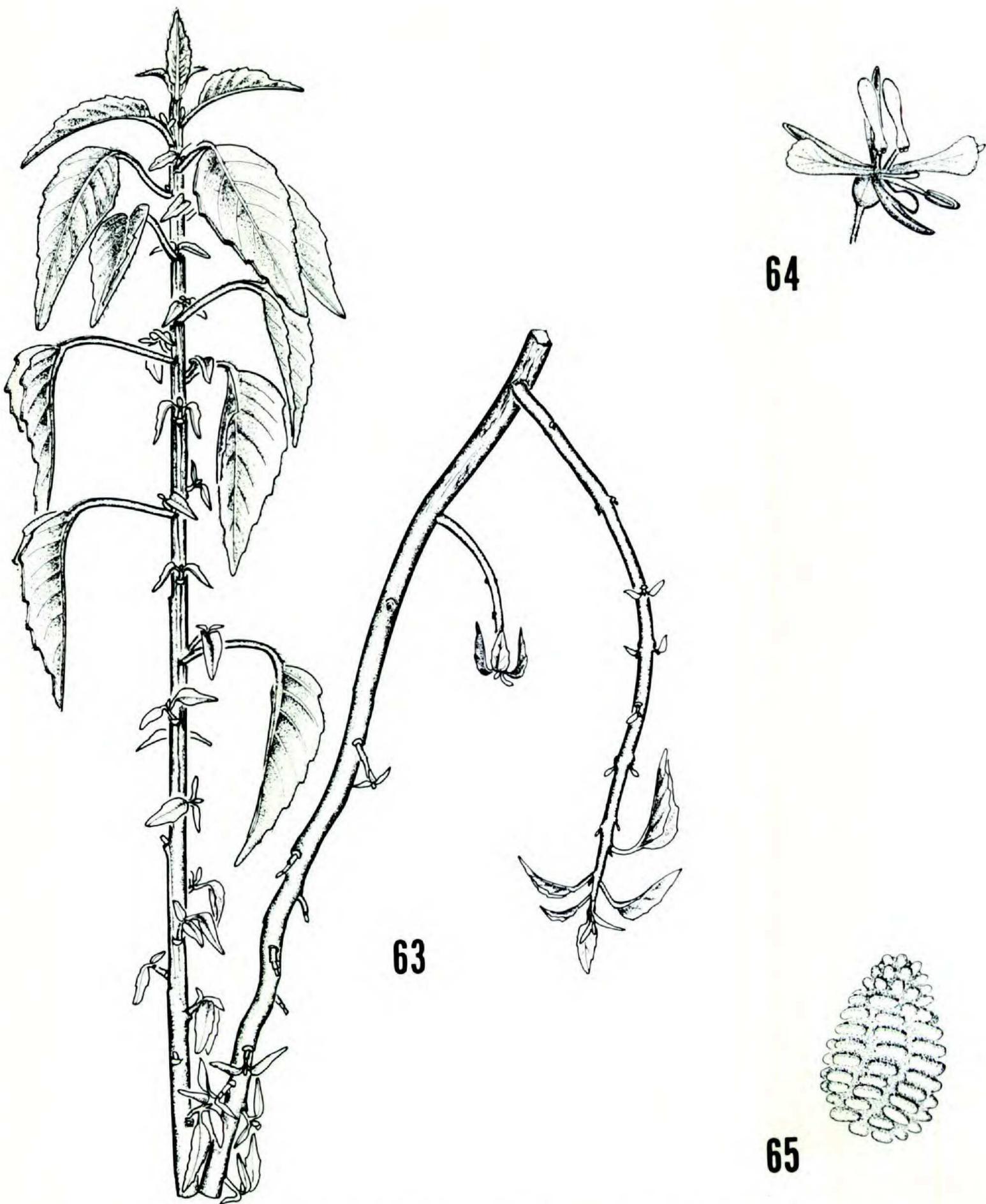
Distribution (Fig. 57): Rare and local on rocky slopes in Sierra Madre Oriental in Nuevo León and San Luis Potosí, Mexico, ca. 600 m elevation. Flowering, October and November.

Additional specimen examined:

MEXICO. SAN LUIS POTOSÍ: En route from San Luis Potosí to Tampico, *Palmer 256 1/2* (BM, MO, NY, POM, S, US).—Most of these specimens include elements of *L. racemosa*. The specimens at BM, MO, POM, and S list the collectors as Parry and Palmer; however, McVaugh (1956: 308) clearly states that Parry had already departed at this time in Palmer's trip.

Lopezia nuevo-leonis occurs at the margins of the range of the genus, and only two populations are known, one from Nuevo León, the other from San Luis Potosí. Both populations are restricted to the Sierra Madre Oriental and in spite of their geographical separation—which may only be apparent since the rugged country between them has seldom been visited by botanists—they are quite similar in morphology.

Lopezia nuevo-leonis is distinguished from the related *L. miniata* by its angular reddish stems; acutely serrate leaves (generally glabrous, fleshy and with fewer veins); pink-reddish flowers; shortly and obtusely auricled upper petals;



FIGURES 63-65. *Lopezia nuevo-leonis*.—63. Branch, $\times 1.2$.—64. Flower, $\times 2.3$.—65. Seed, abaxial view, $\times 23$. All from progeny of the holotype, grown at Stanford University.

oblong or ovoid-ellipsoid and somewhat longer capsules; coarsely rugose-tubercled, blackish and slightly larger seeds. In many of these features, including its reduced chromosome number, it resembles *L. suffrutescens*, an equally restricted endemic of the Sierra Madre Occidental. Because of its chromosome number ($n = 8$) and ecology, we assume that *L. nuevo-leonis* has been derived from populations similar to *L. miniata* as a marginal, ecologically and geographically separated population adapted to more xeric environments.

11. *Lopezia cornuta* S. Wats., Proc. Amer. Acad. Arts 21: 429. 1888. Munz, Brittonia 13: 49. 1961; N. Amer. Fl. II. 5: 18. 1965.

Annual *herbs*, \pm hirsute, especially at base, or subglabrous. *Stems* 1.5–5.5 dm tall, angular. *Leaves* 0.9–4.5 cm long and 0.2–2.4 cm wide, ovate to narrowly lanceolate, rounded or cuneate at base, acute to acuminate at apex, subentire, subglabrous, sparsely ciliate or ciliolate at margins, with 2–7 veins on each side of midrib; petioles (0.1–)0.2–1.2(–2) cm long, hirsute or subglabrous. *Pedicels* 10–30 mm long, ascending, drooping in fruit, \pm hairy. *Sepals* 4–7 mm long and 1–1.5 mm wide, glabrous. *Lower petals* 0.4–9 mm long and 3–6 mm wide, obovate-spatulate, clawed, rounded or subacute at apex, somewhat crenulate, red-streaked in the middle, the rest pink-red; upper petals 4–6 mm long and ca. 1 mm wide, linear-oblong, shortly clawed, somewhat dilated-auricled at base of limb, obtuse, each with two green glands just above claw. *Fertile stamen* 3–4.5 mm long; filament ca. 2.5 cm long; anther ca. 1.5 mm long, whitish. *Staminode* 3–5 mm long, obovate-spatulate, angustate at base, retuse at apex, whitish. *Style* 2–4 mm long; stigma ca. 0.5 mm in diameter, pinkish; ovary obconical-obovoid, longer than wide, angular. *Capsule* (2.5–)3.5–7 mm long, 3–5 mm thick, obovoid-obconical, angular, truncate but horned just below the apex; valves wrinkled-tubercled, separating only slightly, each ending as a broad triangular bent tooth. *Seeds* one or several in each locule, 0.1–2 mm long, ca. 1 mm thick, ovoid, wrinkled and grossly tubercled, dark brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Chihuahua, Cumbre, October 1885, *E. Palmer 367* (GH, lectotype, Munz, Brittonia 13: 80. 1961; isotypes, BM, MEXU, NY, US).

Distribution (Fig. 66): Known only from local populations on moist ledges in pine-oak forests lining the steep barrancas of Sonora, Chihuahua, Sinaloa and Durango, Sierra Madre Occidental, Mexico, 2100–3000 m elevation. Flowering, September to November.

Additional specimens examined:

MEXICO. SONORA: La Mesa Colorada, *Gentry 521* (DS), *521M* (MICH). DURANGO: 13 mi. W of La Ciudad, *Breedlove 15547* (DS); Sandía, *Pringle 10103* (BM, DS, G, GH, IPN, K, M, MEXU, MICH, MO, NY, P, S, UC, US, W, Z); El Salto, *Maysilles 7837* (RSA); NE of El Paraíso, between Villa Union and El Salto, *Ownbey 1955* (BM, MICH, NY, S, UC, US); San Luis del Río, *Breedlove 18830* (CAS). SINALOA: 5 mi. NE of La Cienega, Sierra Surutato, *Breedlove & Kawahara 17050* (CAS); Bufa de Surutato, 3 mi. SE of Los Hornos, *Breedlove & Thorne 18452* (CAS, RSA).

Two groups of populations are recognized in *Lopezia cornuta*. Northern populations (Chihuahua, Sinaloa and Sonora), growing in pine and oak forests, consist of plants that are smaller in all respects than the southern ones (Durango), growing in barrancas and canyons, which are more lush. Accordingly, the whole species displays quantitative variation in length of stems, size of leaves and dimensions of flowers and capsules. The variation is continuous (or overlapping) and the two populations are not divergent enough (contrary to the similar situation in *L. laciniata*) to be recognized as subspecies.

The type of *Lopezia cornuta* belongs to the northern group (with stems to 30 cm; leaves to 3.2 cm long and 1 cm wide; flowers to 5.5 mm long; capsules to 4 mm long). The type locality is the same as that of *L. gracilis*. Vegetatively the

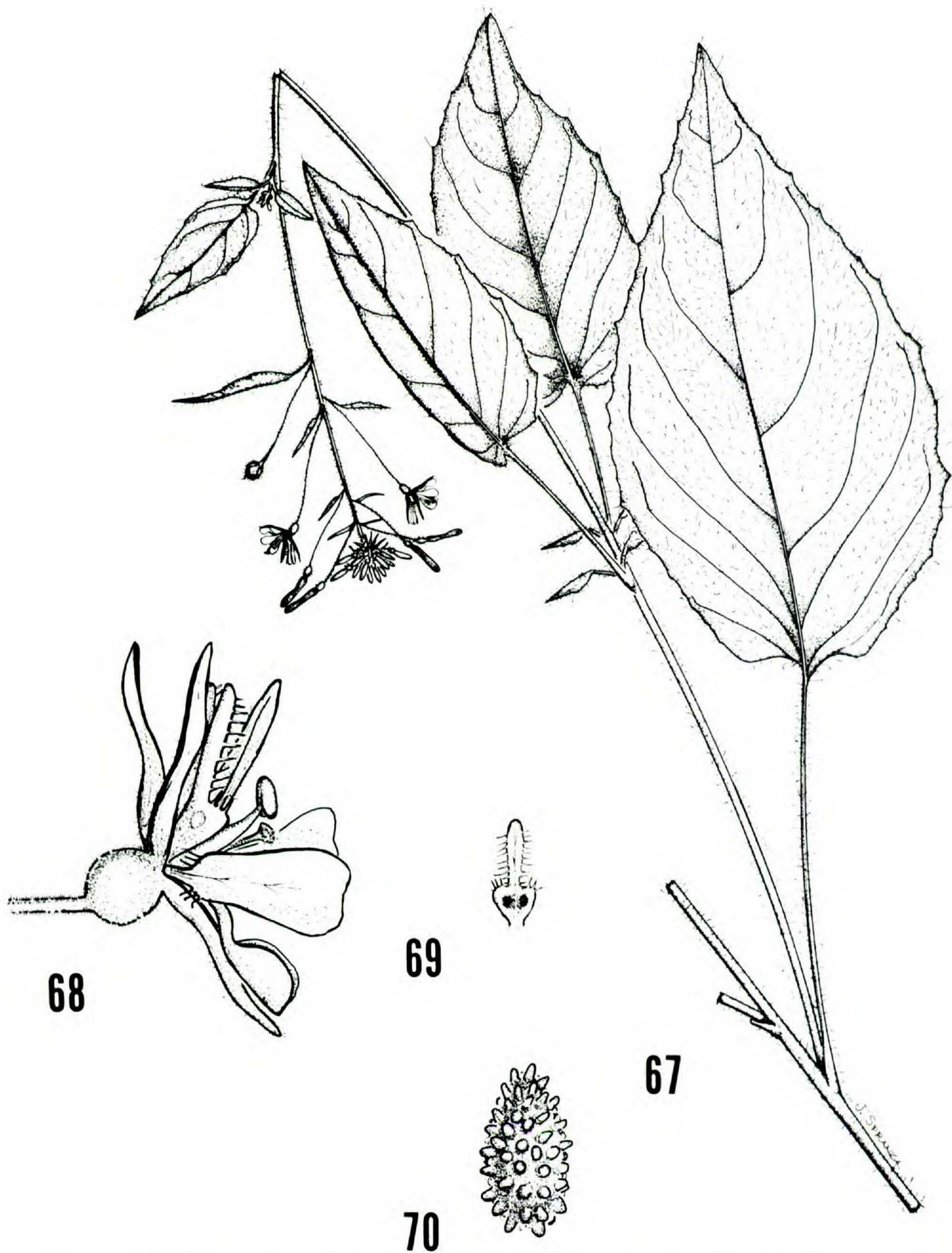


FIGURE 66. Geographical distribution of *Lopezia cornuta* (squares), *L. trichota* (dots), *L. racemosa* subsp. *moelchenensis* (open boxes), *L. conjugens* (filled triangle), and *L. smithii* (open triangles).

northern type and *L. gracilis* resemble each other to a degree, although *L. cornuta* has \pm hirsute and angular stems and generally longer leaves and petioles, and therefore they have sometimes been confused. These species are amply different in the morphology of flowers and fruits as well as in their biology. *Lopezia cornuta* has longer floral parts, its pinkish-red petals, the upper ones with two glands each, its larger, angular and horned capsules, and its coarsely wrinkled-tuberculate seeds. The southern group, on the other hand, consists of plants that are somewhat similar to those of *L. racemosa*. The flower in general and the upper petals in particular are reminiscent of those of *L. racemosa*. In many details, however, *L. cornuta* is quite similar to *L. miniata* (e.g. leaves subentire, lower petals somewhat crenulate, upper petals biglandular). It may have been derived from populations similar to those of *L. miniata*.

12. ***Lopezia ciliatula*** Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 279. 1973.—FIGS. 67–70.

Hirtellous annual *herbs*, \pm gray-green in hue, the hairs incurved or straight. *Stems* 4–9 dm tall; branches obscurely angled. *Leaves* 1–9 cm long and 0.5–5 cm wide, ovate, or oblong-ovate to lanceolate, subcordate to obtuse or broadly cuneate



FIGURES 67-70. *Lopezia ciliatula*.—67. Branch, $\times 66$.—68. Flower, $\times 6.6$.—69. Upper petal, $\times 3.3$.—70. Seed, abaxial view, $\times 26$. All from the type collection.

at the usually oblique or unequal base, acute to acuminate at apex, serrate to serrulate, with 4-8 veins on each side of midrib, hispidulous and glandular, sometimes with a few longer appressed hairs, ciliate; petioles 0.3-6.5 cm long, very narrowly winged, pubescent. *Bracts* 3-25 mm long and 0.5-7 mm wide; pedicels

8–15 mm long, angular or narrowly marginate, spreading or ascending, densely hirtellous and glandular-pubescent. *Flowers* mainly autogamous, retaining the snapping mechanism but the anther soon shedding pollen directly on the stigma, their maturation simultaneous. No visible nectar secretion. *Sepals* 3–4.5 mm long and 0.6–1 mm wide, sparsely hirtellous and glandular-pubescent to subglabrous. *Lower petals* 2.5–4 mm long and 1.5–2 mm wide, oblong-obovate, short-clawed, subcrenulate, long-ciliate near base, white or faint pink; upper petals 2.5–4 mm long and 0.5–0.9 mm wide, narrowly linear-spatulate, slightly narrowed toward base, then broadly obtriangular-obovate, conspicuously auriculate, sessile, obtuse at apex, long-ciliate, with 2 green glands at level of auricles, white, lined with pink. *Fertile stamen* 3–4 mm long; filament winged-dilated except at the twisted apex; anther 1–1.3 mm long, faintly greenish. *Staminode* white, 2.5–4 mm long and 1.5–2 mm wide, suborbicular or obovate-spatulate, \pm emarginate at apex, abruptly narrowed into a rather long claw, white or pale pink. *Style* white, 2.5–3.5 mm long; stigma 0.25–0.5 mm in diameter; ovary globose to ellipsoid, pubescent with erect glandular and eglandular hairs. *Capsule* 1.5–3.5 mm long, 1.5–3.5 mm thick, subglobose, with an admixture of glandular and eglandular hairs. *Seeds* 0.8–1 mm long, 0.4–0.5 mm thick, ovoid, distinctly papillose-tubercled, dark brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Sinaloa, Sierra Surutato, Cañon de Tarahumares between Arroyo Verde and Rancho Tarahumares, steep north-facing slope, ca. 1100 m elevation, 27 February 1968, *D. E. Breedlove 15921* (DS).

Distribution (Fig. 34): Known only from two localities, steep-walled canyons with *Bursera* and *Ipomoea*, in the Sierra Madre Occidental, Durango and Sinaloa, Mexico, 1100–1250 m elevation. Flowering, February and March.

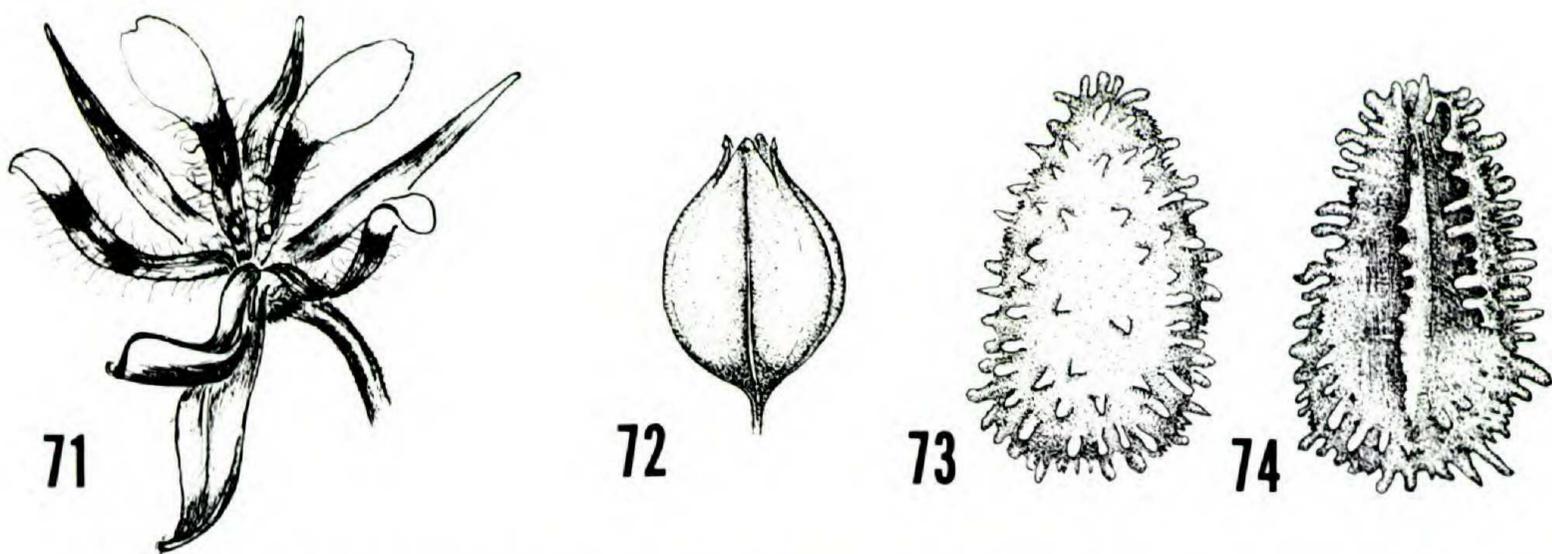
Additional specimens examined:

MEXICO. SINALOA: Cañon de Tarahumares between Arroyo Verde and Rancho Tarahumares, *Breedlove 16439, 19107* (both CAS); mouth of the Canon Tarahumares at El Alamo, *Breedlove 19058* (CAS). DURANGO: Steep side canyons of the barranca of the Río Tamazula between La Bajada and La Junta, 1250 m, *Breedlove 24491* (CAS).

Lopezia ciliatula is easily distinguishable from the related biglandular species by such features as its small flowers, sessile and basally winged-auricled upper petals, ciliation of petals, pubescence of petioles, pedicels and capsules. It has the same chromosome number as *L. cornuta*, but in overall morphological appearance it resembles *L. miniata*, from which it may have been derived. Curiously, it is known only from the same two areas as *L. suffrutescens*.

13. *Lopezia trichota* Schlecht., *Linnaea* 12: 273. 1838. Munz, *Brittonia* 13: 85. 1961; *N. Amer. Fl. II.* 5: 21. 1965.—FIGS. 71–74.

Subglabrous perennial *herbs*. *Roots* thick, tuberous, fleshy. *Stems* 2–10 dm tall, to 6 mm thick, angular. *Leaves* fleshy, 1–4.5(–5.5) cm long and 0.3–2.5(–3.3) cm wide, rounded or obtuse and \pm asymmetrical at base, acute at apex; lower leaves ovate, serrate or serrulate, glabrous, few-veined; the upper ovate to rarely lanceolate, serrulate or subentire, subglabrous but somewhat puberulent at margins or sometimes strigulose along midrib; petioles 0.2–2.5 (–3) cm long, ca. 0.1 cm thick, slightly pubescent to glabrous. *Inflorescence* \pm puberulent-strigulose;



FIGURES 71-74. *Lopezia trichota*.—71. Flower, $\times 3.2$.—72. Capsule, $\times 3.2$.—73. Seed, abaxial view, $\times 21$.—74. Seed, adaxial view, $\times 21$. All from Rzedowski 6896 (DS).

bracts 2-15(-25) mm long and 0.5-2(-4) mm wide, \pm ciliolate at margins, puberulent; pedicels 6-20 mm long, patent to almost erect, pubescent to subglabrous. *Flowers* white with deep purplish-red marking. *Sepals* 5-7.5 mm long, and 0.7-2 mm wide, \pm crisp-pubescent or slightly puberulent to glabrous. *Lower petals* 4-5.5 mm long and ca. 1 mm wide, linear, obtuse and glabrous at apex, densely ciliate with curly hairs along margins; upper petals 4-7.5 mm long and 1.5-3 mm wide, obovate-spatulate, clawed for almost one-third of their length, rounded or somewhat retuse at apex, ciliate along blade except for the uppermost part, white toward apex, red below; claw \pm ciliate, bearing a single gland but sometimes with an adjacent second (reduced) one. *Fertile stamen* 4-5 mm long, purplish-red; filament fleshy, glabrous; anther ca. 2 mm long. *Staminode* 4-6 mm long, and 2-3.5 mm wide, spatulate with a broad blade, clawed-narrowed at base, retuse and mucronulate at tip, purplish-red, glabrous. *Style* 4-5 mm long, crisp-pilose; stigma ca. 0.5 mm in diameter; ovary 1.5-3 mm long, 1-2 mm thick, subglobose, \pm crisp-pubescent or puberulent to glabrous. *Capsule* 4-7 mm long, 3-6 mm thick, oblong-ovoid to globose, ascending, subglabrous; valves coriaceous, intact or open at apex only. *Seeds* ca. 1 mm long, ca. 0.6 mm thick, subovoid, with wing-like margins, coarsely tubercled and wrinkled, black. Gametic chromosome number, $n = 10$.

TYPE: Mexico, Hidalgo, Mineral del Monte (ca. 25 km E of Ixmiquilpán), Cuesta Blanca, rocky places, August 1836, *C. Ehrenberg* 626 (HAL).

Distribution (Fig. 66): Common on dry slopes and barrancas, chiefly in pinyon-juniper woodland, in widely scattered localities from Chihuahua to Puebla, Mexico, (1200-)1600-2700 m elevation. Flowering, July to October.

Representative specimens examined:

MEXICO. CHIHUAHUA: Mts. near Chihuahua, *Pringle* 733 (BM, G, GH, K, MEXU, MO, NY, P, RSA, S, UC, US, W); San Mateo to Quasarachi, *Goldman* 147 (GH, NY, US); Sierra Azul, SW of Mapula, *Pennel* 18656 (NY, US). **DURANGO:** 9 mi. SE of Santiago Papasquiari on road to Canatlán, *Breedlove* 15542 (DS); 16 mi. W of Durango on Mex. Hwy. 40, *Breedlove* 14392 (DS); Durango and vicinity, *Palmer* 588 (BM, G, GH, MO, POM, S, UC, US). **SAN LUIS POTOSÍ:** Cerro Verde, W of San Lorenzo, *Rzedowski* 6856 (DS, IPN, MEXU, MICH, RSA, TEX); NE of Laguna Seca, *Rzedowski* 6330 (IPN); Convalli, *Schaffner* 641 (GH, NY). **HIDALGO:** NE of Pachuca, *Rzedowski* 17059 (IPN, MEXU, MICH); Cerro Ventoso, Pachuca to Real del Monte, *Rzedowski* 20575 (DS), *Pringle* 9798 (GH, MO, NY, US, Z), *Rose* &

Painter 6692 (US); Cuesta de Texquedo, Tasquillo to Zimapán, *Moore 1656* (GH); Above Metzquitlán, to Zacualtipán, *Moore 5405* (UC); Sierra de Guadalupe, near Cuauhtepac, *Galicia, 1962* (DS, IPN, TEX). MICHOACÁN: Near Morelia (Punguato), *Arsène 6644* (MO, US); Guanajuato to Dolores Hidalgo, *Solbrig & Ornduff 4516* (RSA, UC). MÉXICO: Near Presa de la Concepción, Tepotzotlán, *Rzedowski 22901* (IPN); Huixquilucán, la Presa "El Capulin," *Rzedowski 25863* (DS). DISTRITO FEDERAL: Santa Catarina, near Los Reyes, *Paray 1591* (IPN); Sierra del Guadalupe, *Miranda 3850* (MEXU). PUEBLA: San Luis Tultitlanapa, *Purpus 3398* (BM, GH, MO, NY, UC, US); Villa Juárez, *Galván, 1963* (IPN).

Lopezia trichota is quite uniform morphologically and very distinctive biologically. Though maintaining the snapping mechanism and protandrous, it is very likely self-pollinated to some degree as well. The mature capsules are \pm indehiscent, their coriaceous valves frequently remaining almost intact; they might, therefore, be dispersed by water. In accordance with its dry habitat, the capsule probably needs some moisture for dehiscing (partly hygrochastic); all other species of *Lopezia*, as far as known, have xerochastic fruits. *Lopezia trichota* is vegetatively propagated by its unique tubers, which are thick, fleshy and bulbous, and very different from those of other tuberous *Lopezia* species; such tubers are an evident adaptation to dry habitats. The plant goes dormant for several months, like many cryptophytes, and starts sprouting in the early summer (rainy season). Dry conditions enhance its flowering. Another distinctive feature of this species is the number of glands on the upper petals. Usually there is a single one, yet sometimes a second smaller one is developed. This suggests that its ancestors might have had two glands on each of the upper petals. Otherwise the flower, in general, resembles that of *L. racemosa*.

Lopezia trichota is restricted to central Mexico, east of the Sierra Madre Occidental and north of the Sierra Madre del Sur. Its distribution is \pm interrupted (no records from Tlaxcala, Zacatecas, Aquascalientes and Queretaro), presumably because of its specific ecological demands.

14. *Lopezia racemosa* Cav., *Icones 1: 12, t. 18. 1791*. Munz, *Brittonia 13: 86. 1961*; N. Amer. Fl. II. 5: 22. 1965.

Annuals or perennials, hirsute, strigulose, or mixed strigulose and glandular-pubescent to subglabrous. *Stems* erect or ascending or decumbent and rooting at nodes, subterete, 1–15 dm tall. *Leaves* variable in size, shape and pubescence; lower leaves 1–8 cm long and 0.5–4.5 cm wide, ovate to narrowly lanceolate, acute or cuneate to rounded at base, sometimes acuminate, subacute or sometimes subacuminate at apex, mucronulate, acutely dentate or serrate to shallowly or remotely so, with 4–11 veins on each side of midrib, densely hirsute or strigose to sparsely so, with hairs usually appressed but sometimes spreading, equally pubescent on both sides to more densely so below especially along veins, sometimes subglabrous; upper leaves 0.5–5 cm long and 0.15–2.5 cm wide, ovate to very narrowly lanceolate, acute or cuneate to obtuse at base, usually acute or acuminate at apex, serrate to subentire, with (0–)3–7 veins on each side of midrib; petioles 0.1–4 cm long, infrequently narrowly winged, strigulose or more rarely subglabrous. *Bracts* 2–25(–30) mm long and 0.5–9(–12) mm wide; *pedicels* 6–24(–30) mm long, spreading to ascending-erect in flower, drooping to ascending in fruit, sometimes divaricate but bent upwards, strigulose or puberulent to

glabrescent. *Flowers* strongly protandrous, but in some strains self-pollinating in due course. *Sepals* 3.5–7.5 mm long and 0.5–2 mm wide, glabrous or sparsely hirsute with few long hairs especially toward apex, sometimes glandular-puberulent. *Petals* variable in size, color and inclination, whitish or pinkish-lilac to pink or red or even purplish, sometimes white-lilac or orange-red, somewhat darker near the center (lower petals) or near tip (upper petals) and paler below; lower petals (3.5–)4–9(–10) mm long and (1.5–)2–5.5(–6) mm wide, oblong-obovate or spatulate to obovate or even oblate, acuminate symmetrically or not, clawed with claw as long as or longer than blade, round and entire or nearly so at apex; upper petals 4–8.5 mm long and 0.7–2 mm wide, linear-oblongate to oblong-oblongate, erect, clawed with claw shorter than blade and ciliate to hardly so, \pm obtuse and entire at apex, blade dilated to obtusely short-auricled at base, bearing a single gland; gland tiny or prominent, variable in shape, usually green, sometimes pink. *Fertile stamen* 3–5.5 mm long; anther 1–2 mm long, greenish-grey to bluish or even purplish. *Staminode* 3–5(–6) mm long and 2–3 mm wide, generally obovate, abruptly narrowed into a linear claw, \pm retuse at apex, whitish to pink or red. *Style* 2.5–4.5 mm long, glabrous; stigma (0.4–)0.5–1.1(–1.7) mm across, white to pink; ovary subglobose, glabrous. *Capsule* (2–)3–7 mm long, 2–5 mm thick, usually globose, sometimes obpyriform and subclavate or ovoid or oblong-ellipsoid, rarely compressed at apex, glabrous. *Seeds* (0.8–)0.9–1.2(–1.3) mm long, (0.6–)0.7–0.8(–0.9) mm thick, ovoid, irregularly rugose- or muricate-tubercled, brown. Gametic chromosome numbers, $n = 10$ (11), 20.

Distribution (Figs. 66, 75): Widespread and common in the pine-oak zone but also common as a roadside weed and as a weed in *milpas*, from Durango (Chihuahua?) and San Luis Potosí in Mexico south to El Salvador, 1100–3300 m elevation. *Lopezia racemosa* occurs sympatrically with *L. miniata* at a number of localities. Flowering, mainly from August to March, although occasional individuals may be found in flower in any month of the year.

This extraordinarily polymorphic species includes one well marked geographic race, the tetraploid derivative subsp. *moelchenensis* of Chiapas, Mexico, and northwestern Guatemala. As reported elsewhere (Plitmann, Tai & Raven, 1974), a tetraploid plant of subsp. *racemosa* has likewise been found in Chiapas, and interploid hybridization between the two subspecies, with incomplete pollen sterility, is apparently frequent. Intermediate forms between these two are, for example: *Standley* 22876 from El Salvador; *Brenckle* 47280, 47396, *Kellerman* 4816 from Guatemala; *Matuda* 5212, *Shilom Ton* 651, 758 from Chiapas. These specimens, although usually hirsute-pubescent, have leaves, colors, racemes and sometimes capsules or seeds as in subsp. *moelchenensis* but otherwise resemble subsp. *racemosa* (in habit, pubescence, floral morphology, and pollen). Other specimens share some features of subsp. *moelchenensis* (color of stems or flowers, serration of leaves, shape of capsule, racemes or general habit); those are considered as transitional convergent forms of subsp. *racemosa*. Collections of such subsp. *racemosa*-like plants with a few traits of subsp. *moelchenensis* are: *Shilom Ton* 1482, *Breedlove* 7134, 7155, 11425, 12622, 8759, *Breedlove & Raven* 13294/3,

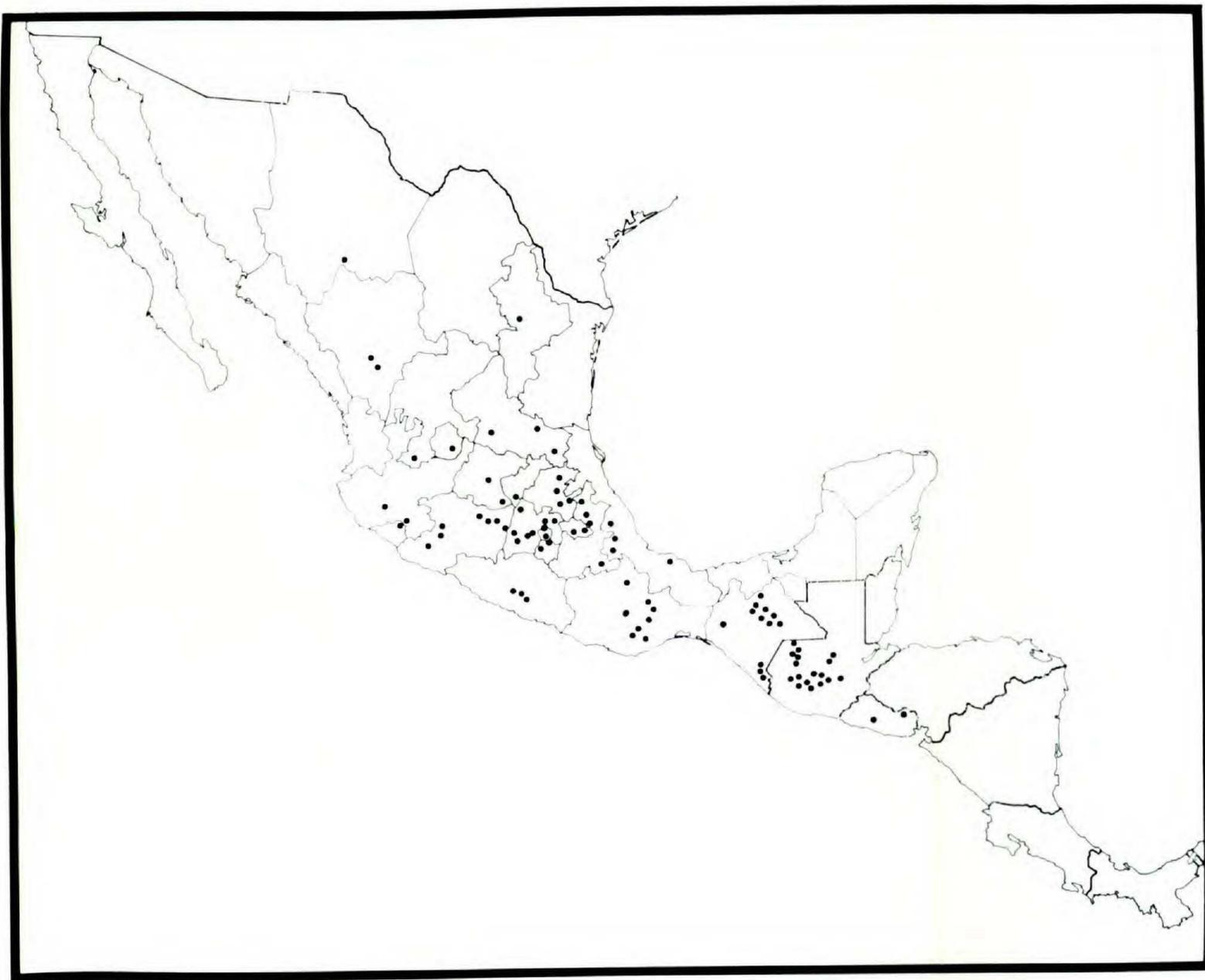


FIGURE 75. Geographical distribution of *Lopezia racemosa* subsp. *racemosa*.

Kerber 391, Matuda 2383, 2540, 479, 697, Miranda 4975 from Chiapas; *Skutch 1520, Kellerman 7613, Rodríguez 2041, Beaman 3949* from Guatemala; *Standley 22804* from El Salvador; and probably *Rzedowski 18568* from Guerrero and *Moore 2401* from Hidalgo.

Further indication of actual hybridization in the field is provided by *Shilom Ton 651*, from Paraje Pahal Ton, Municipio Tenejapa, Chiapas. This collection is of tall plants with the erect stems generally associated with *Lopezia racemosa* subsp. *racemosa* but with other features as in subsp. *moelchenensis*. Two plants were grown in the greenhouse from seeds removed from this specimen. Both of these were about 1.5 m tall, with almost simple, erect stems, relatively narrow but fleshy leaves, and orange flowers as commonly found in subsp. *moelchenensis*. One of these plants was hirsute, the other glabrescent.

Crossing experiments showed that *Lopezia racemosa* subsp. *racemosa* is comprised of lines of high and low crossability with each other. On the other hand it is amazing that many strains were quite easily crossed with the tetraploid *L. racemosa* subsp. *moelchenensis*. In such triploid hybrids, the characteristics of the tetraploid subsp. *moelchenensis*, not surprisingly, are predominant over those of the diploid subsp. *racemosa*.

KEY TO THE SUBSPECIES

- Stems ascending or erect, rarely decumbent; leaves not fleshy, pubescent or rarely subglabrous, ovate or lanceolate; petals \pm orange; pollen almost entirely 3-porate; wide-spread 14a. subsp. *racemosa*
- Stems decumbent, rooting at the nodes; leaves fleshy, subglabrous, mostly narrowly lanceolate; petals mostly without orange tinge; pollen with a high proportion of 4-porate and some 5-porate grains; Chiapas, Mexico, and Guatemala 14b. subsp. *moelchenensis*

14a. *Lopezia racemosa* subsp. *racemosa*.—FIGS. 12–13.

Lopezia mexicana Jacq., Ic. Pl. Rar. 1: pl. 203. 1793.

Lectotype: Jacq., Pl. Rar. 2: t. 203. 1792–3. Cultivated from seeds from Mexico, probably of the same stock of the original *L. racemosa* (W—Hort. bot. Vind., Hb. Jacq., authentic?).

Pisaura automorpha Bonato, Pisaura 7, t. 1. 1793. Type: G.4505 (W, cultivated from the authentic?).

Lopezia hirsuta Jacq., Obs. Bot. 5: 5, pl. 15, fig. 4. 1796. Lectotype: Jacq., Obs. Bot. 5: pl. 15, fig. 4. 1796. Munz, Brittonia 13: 88. 1961; N. Amer. Fl. II. 5: 23. 1965.

Lopezia mexicana Jacq. var. *hirsuta* (Jacq.) Willd., Sp. Pl. 1: 18: 1797.

Lopezia coronata Andrews, Bot. Rep. 8, t. 551. 1808. Lectotype: Andrews, Bot. Rep. 8, t. 551. 1808. Cultivated from Mexican material of unknown origin in the conservatory of the Countess de Vandes, "Introd. 1805 by Messrs. Lee and Kennedy" (Aiton & Aiton, Hort. Kew. ed. 2, 1: 10. 1810); (E, authentic?). Munz, Brittonia 13: 88. 1961; N. Amer. Fl. II. 5: 22. 1965.

Lopezia axillaris Thunb. ex Schweigger, Königsberger. Arch. Naturwiss. Math. 1: 236. 1811–12. Schweigger, Enum. Hort. Regiomont 44, adnot. 26. 1812. Type: Cultivated (UPS? Non vidimus).

Lopezia mexicana Jacq. var. *coronata* (Andr.) DC., Cat. Hort. Monsp. 39. 1813.

Lopezia cordata Hornem., Hort. Hafn. 949. 1815. Type: Cultivated from seeds introduced in 1813 (C? Non vidimus).

Lopezia minuta Lag., Gen. & Sp. Nov. 1. 1816. Type: "Praedicto nomine accepimus ex Hort. Paris ann. 1815" (P? Non vidimus).

Lopezia oppositifolia Lag., Gen. & Sp. Nov. 1. 1816. Type: Cultivated from seeds sent by D. V. Cervantes in 1814 (= *L. annua* hortul.) (G-DC? Non vidimus).

Lopezia minima Lag. ex Schrank, Nova. Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 9: 92. 1818. Type: Unknown. Munz, Brittonia 13: 90. 1961.

Lopezia integrifolia DC., Prodr. 3: 62. 1828. Type: Mexico, *Alaman* (G-DC, lectotype, Munz, Brittonia 13: 87. 1961; isolectotype, US).

Lopezia lineata Zuccarini, Pl. Nov. Cogn. 2: 339. 1838. Type: Cultivated in München, "Crescit in Imperio Mexicano, unde semina misit clar. de Karwinski" (M, ex herb. Zucc., 1835, probably from the authentic material).

Lopezia haematodes Kunze, Linnaea 17: 579. "1843" (1844). Type: November or December, 1843, Hort. Lips. (BM, lectotype, from the cultivated authentic material which had been grown in 1842–43 in hort. bot. univ. Lips.; HAL, syntype, coll. by G. Kunze in Nov. 1843, as plant cult. in hort. bot. Lips., from Mexican seeds sent by Schleiden, 1843).

Lopezia albiflora Schlecht., Linnaea 24: 696. 1851. Type: Cultivated in hort. Hal. Sax. (HAL? Non vidimus).

Lopezia angustifolia B. L. Robins., Proc. Amer. Acad. Arts 27: 168. 1893. Type: Mexico, San Luis Potosí, Las Canoas, 30 October 1891, C. G. Pringle 3990 (GH; isotypes, BM, F, G, IPN, K, M, MO, NY, P, POM, S, UC, US, W, Z). Munz, Brittonia 13: 90. 1961; N. Amer. Fl. II. 5: 23. 1965.

Lopezia foliosa T. S. Brandege, Zoö 5: 250. 1908. Type: Mexico, Veracruz, Barranca de Tenampa, near Zacuapán, November 1906, C. A. Purpus 2303 (UC; isotypes, BM, GH, MO, NY, P, US).

Lopezia elegans Rose, Contr. U. S. Natl. Herb. 12: 298, fig. 40. 1909. Type: Mexico, San Luis Potosí, Álvarez, 28 September–3 October 1902, E. Palmer 159 (US 397,706; isotypes, GH, MO, NY, UC).

- Lopezia glandulosa* Rose, Contr. U. S. Natl. Herb. 12: 298, fig. 41. 1909. Type: Mexico, Zacatecas, between Bolaños and Guadalajara, 20 September 1897, J. N. Rose 3034 (US 301,991. Isotype, NY).
- Lopezia parvula* Rose, Contr. U. S. Natl. Herb. 12: 300, fig. 44. 1909. Type: Mexico, Durango, near La Providencia, November 1898, E. W. Nelson 4987 (US 333,016. Isotype, GH).
- Lopezia pringlei* Rose, Contr. U. S. Natl. Herb. 12: 300, fig. 45. 1909. Type: Mexico, Oaxaca, Sierra de San Felipe, 25 September 1894, C. G. Pringle 6005 (US 461,987. Isotypes, BM, F, G, IPN, M, MEXU, MICH, MO, NY, P, RSA, S, UC, W, Z).
- Lopezia corymbosa* Sprague & Riley, Jour. Bot. 62: 15. 1924. Type: Guatemala, Alta Vera Paz, Cobán, November 1885, von Türckheim 766 (K. Isotypes, GH, NY, P, US).

Hirsute, strigulose, or mixed strigulose and glandular-pubescent to subglabrous annual or perennial *herbs*. Stems ascending or erect, rarely decumbent, pubescent or subglabrous. Leaves not fleshy, pubescent or more rarely subglabrous, 0.5–8 cm long and 0.15–4.5 cm wide, ovate or lanceolate, acute or cuneate to obtuse at the base, acutely dentate or serrate to shallowly and remotely so, the teeth usually lacking dark clusters of “oil cells” (Stein, 1915) at the tips. Pedicels 0.6–2.4(–2.7) cm long. Petals whitish or pinkish-lilac to pink or red or even purplish, sometimes lilac-white or orange-red. Pollen almost entirely 3-porate. Gametic chromosome number, $n = 10$ (11, 20).

Lectotype: Cav., Icones t. 18. 1791, based upon plants grown in the Royal Botanic Garden at Madrid. Probable authentic material: “*L. racemosa* Cav., cult. in hort. Carolin., 1796,” Gmelin (W) and “Gmelin in 1790” (W); “*L. racemosa*, ex hispania misit D. Cavanilles 1790–91, Herb. d’Antoine Laurent de Jussieu” (P); “*L. racemosa* Hort. Chelseam., 1796” (BM; *L. racemosa* was grown at the Apothecaries Garden, Chelsea from 1792 onward from seeds received from Madrid; Bot. Mag. 7: 254. 1797); “*L. racemosa*, Hort. R. Matr.” (M; according to Munz, 1961: 87: “2 sheets, one dated 1802 and 1814, the other ‘Herb. Cav.’; they are labelled *L. mexicana* Jacq., *L. racemosa* Cav., *Pisaura automorpha* Bonata, *Entomanthus* [sic] Sesse & Moc.; it would seem that Cavanilles’ name *racemosa* and Jacquin’s name *mexicana* are based on the same material, or same lot of seed from Mexico”).

Distribution (Fig. 75): That of the species. Flowers mostly between April and November (the rainy season), although occasional individuals may be found in flower during any month of the year.

Representative specimens examined (additional to those listed by Munz, 1961):

MEXICO. QUERÉTARO: 1 mi. NE of Amealco, Breedlove 7213 (DS). GUANAJUATO: Santa Rosa Mts., Dugés 308b (GH); Sierra NE of Guanajuato, Ripley & Barneby 13365 (DS, NY); 10 mi. E of Jeracuaro, Breedlove 7214 (DS). AGUASCALIENTES: 21 mi. W of Aguascalientes, McVaugh & Koelz 153 (MICH). SAN LUIS POTOSÍ: Near San Luis Potosí, Parry & Palmer 256 1/5 (BM, MO, NY, US); Potrerillos, Municipio of Xilitla, Rzedowski 10001 (DS, IPN, P); 2 km N of Puerto del Hambre, Municipio of Cd. del Maíz, Rzedowski 8310 (IPN); Sierra de Álvarez, near Puerto Huerta, Rzedowski 5269 (IPN). HIDALGO: Between Pachuca and Real del Monte, M. E. Moore 1565 (BM, GH, MICH, UC); 9 km W of Huauchinango, Rzedowski 23425 (DS); 10 mi. E of Huichipán, Breedlove 7208 (DS); 4 mi. SW of Atotonilca, Breedlove 7203 (DS); 30 mi. S of Jacala, Breedlove 7205 (DS); Chapulhuacán, Sharp 441747 (RSA); Zimapan, Coulter 179 (GH, K). JALISCO: SE slopes of Nevado de Colima, Atenguique to Tonila, McVaugh 11725 (MEX, MICH, RSA, US); Sierra de Manatlán, SE of Autlán near Aserradero El Cuartón, McVaugh 13830 (MEX, MICH, RSA). COLIMA: Near Volcán Colima, H. Ross 495 (M). MICHOACÁN: 47 mi. E of Morelia, Breedlove 7224 (DS); 20 mi. E of Morelia, Breedlove 7225 (DS); 17 mi. S of Zinapecuaro, Breedlove 7222 (DS); Tancitaro,

Leavenworth & Hoogstraal 1114 (MO); 2 km SE of San Miguel del Monte, *Rzedowski 25173, 25184* (both DS). GUERRERO: Cerro Alquitrán, near Mazatlán, *Rzedowski 23628, 23649, 23652* (all DS); Tlacotepec, Cerro Teotepec, *Rzedowski 18568* (IPN, MEXU, MICH); 3 km S of Amojileca, *Rzedowski 23560* (IPN). MÉXICO: 18 mi. SW of Toluca, *Molseed 546* (DS); 20 km NE of Texcoco, *Rzedowski 21423* (DS); 5 km N of Mesón Viejo, Municipio of Temascaltepec, *Rzedowski 21694, 21708* (DS); 15 mi. E of Zitacuaro, *Breedlove 8075* (DS); city limits of Lerma, *Breedlove 7201* (DS); S city limits of Amecameca, *Breedlove 15445* (DS); 28 mi. SE of San Juan del Río, *Breedlove 15451* (DS); Coyotepec, La Marquesa to Chalma, *Rzedowski 17244* (IPN); near the Pyramid of Calixtlahuaca, *Barkley, Westlund & Paxon 675* (TEX); Valle de Bravo, *Matuda et al. 26937* (MEXU). DISTRITO FEDERAL: San Angel, *E. G. Smyth 205* (US); La Venta, *Lyonnet 1432* (US); Cerro de Santa Catarina, *Paray 70* (IPN). MORELOS: Lagunas de Zempoala, *Breedlove 15835* (DS), *Holguin s.n.* (IPN), *Langman 2672A* (US), *Rzedowski 21623* (DS); Cuernavaca, *T. Beelin 50* (IPN); Cuautla, *B. Downing 160* (MICH). TLAXCALA: E of Ciudad Tlaxcala, *Ripley & Barneby 13636* (DS); between San Cristóbal and Calpulalpán, *Sohns 571* (MICH, US). PUEBLA: 7 mi. N of Atotonilco, *Ripley & Barneby 13626* (DS); Alrededores de Xicotepec de Juárez, *L. Gonzales Quintero 767* (DS); Puerta del Emperador, *Sharp 44404* (RSA); San Luis Tultitlanapa, *Purpus 4193* (UC); Huauchinango, *Rudd 2012* (DS); Chaltetela, 3 km NE of Zacapoaxtla, *Giovannini* (DS). VERACRUZ: Orizaba, *Botteri 932* (BM, K, P, RSA), *F. Muller 207* (W); Veracruz to Orizaba, *F. Muller 1573* (K); near Las Vigas, *Dodds 97* (MICH); Maltrata, *Matuda S-134* (MICH); Jalapa, *Ch. L. Smith 1786* (NY), *Schiede & Deppe 536* (MO, NY); near El Puerto, above Acultzingo, *Sharp 44832* (RSA); 5 km SE of Teocelo, *Garcia Saucedo 117* (DS); La Sabana, S of Volcán de San Martín Tuxtla, *M. Sousa S.3035* (MEXU). OAXACA: Monte Albán, *Conzatti 4858* (MICH); Cordillera, Mixteca Alto, *Galeotti 3060* (G, P); 15 km S of Sola de Vega, *Rzedowski 21324, 21343* (DS); San José del Pacífico, municipio of Miahuatlán, *Rzedowski 21003* (DS); on road from Teotitlán del Camino to Huautla, *Breedlove 15769* (DS); 15 mi. SE of Tamazulapán, *Breedlove 7186* (DS); 16 mi. N of San Gabriel, *Breedlove 9882* (DS); 1 mi. E of Ixtlán de Juárez, *Breedlove 7179* (DS); 1 mi. NW of Tamazulapan, *Breedlove 7191* (DS); 5 mi. NE of Sola de Vega, *Breedlove 8024* (DS); W slope of Mt. Zempoaltepec, *Nelson 595* (US); from Chiquihuitlán to Santa Ana Portezuelo, *Conzatti 3854* (MEXU, US). CHIAPAS: Paraje of Matsab, Municipio of Tenejapa, *Breedlove 12684* (DS); Municipio of Zinacantán, *Laughlin 2936* (DS); Colonia 'Ach'lum, Municipio of Tenejapa, *Ton 1362* (DS); near Piedra-citas, Municipio of Chamula, *Breedlove 7128* (DS); NW side of Cerro Santa Cruz, Municipio of Chenalho, *Ton 1864* (DS); 7 km NW of Pueblo Nuevo Solistahuacán, Municipio of Jitotol, *Raven & Breedlove 19806* (DS); summit of Cerro San Cristóbal, Municipio of San Cristóbal de las Casas, *Breedlove & Raven 13294/3* (DS); Amatenango del Valle, Municipio of Amatenango del Valle, *Ton 1482* (DS); Fenix, *Purpus 10202* (NY, UC, US); Mt. Tacaná, *Matuda 2383* (MEXU, MICH); Mt. Ovando, *Matuda 2540* (MEXU, MICH); Fraylesca, near Siltepec, *Matuda 5212* (MEXU, TEX).

GUATEMALA. HUEHUETENANGO: Jacaltenango, *E. W. Nelson 3590* (US); Sierra de los Cuchumatanes, near San Juan Ixcay, *Beaman 3949* (DS, GH, TEX, UC); 8 km W of Aguacatán, *Williams, Molina & Williams 21861* (G); Sierra de los Cuchumatanes, 3 km N of Chiantla, *Williams & Williams 21727* (G); road to Barillas, Municipio of Barillas, *Breedlove 8759* (DS). TOTONICAPÁN: 5–10 km N of San Carlos, *Williams, Molina & Williams 22570* (G); San Cristóbal, *Tejada 257* (US). QUEZALTENANGO: Near Santa Maria, *Naxon & Hay 3570* (US); Cuesta del Caracol, N of San Juan Ostuncalco, *Williams, Molina & Williams 22744* (G); San Martín, *Shannon 262* (K, US). SANTA ROSA: Volcán Jumaytepeque, *Heyde & Lux 4337* (G, GH, K, M, NY, US). ALTA VERAPAZ: Cobán, *J. D. Smith 1681* (G, M, MO), *H. Johnson 41* (NY), *Türkheim 367* (BM, P). QUICHE: Nebaj, *Skutch 1894* (A). SACATEPÉQUEZ: Volcán de Agua above Santa Maria de Jesus, *Standley 59386* (NY), *Bell & Duke 16965* (MICH); Pachali near San Lucas Sacatepéquez, *Anderson 4614, 4614A* (MO); 4 mi. NW of Ciudad Vieja, *Breedlove 11425* (DS). SUCHITEPÉQUEZ: Volcán Atitlán, *Skutch 1520* (GH). SOLOLA: Near Lake Atitlán, *Williams, Molina & Williams 25341* (a peculiar form; DS). CHIMALTENANGO: Near Parramos, *Standley 59882* (POM); Soledad, Volcán Acatenango, *Hunnewell 17188* (GH); Chichavac, *Skutch 11* (US). GUATEMALA: Near San Juan Sacatepéquez, *Standley 59271* (POM); Camino del Sapote, *Bernoulli 234* (G, K, NY); Volcán Pacaiya, *Brenckle 47280* (NY, S) *47396* (RSA); San Vincente Pacaya, *Tonduz 457* (G, MO, US). JALAPA: Between Jalapa and Paraíso, *Standley 77344* (POM).

EL SALVADOR. SAN SALVADOR: Volcán San Salvador, *Williams & Molina 15103* (a peculiar form; GH), *Standley 22876* (GH, NY, US), *22804* (GH, US), *Calderón 611* (US). MORAZÁN: Cordillera Miramondo, *Molina, Burger & Wallenta 16858* (W).

CULTIVATED: "*Lopezia mexicana*, hort. bot. Erlangensis 1795 & 1805" (M); "*Lopezia racemosa* hab. prope Mexico," hort. bot. Monac. 1815 (M, herb, Zuccarini; actually "*L. coronata*"); Jardin Pl. de Paris, 1818, M. Perrottet (G, probably from the authentic stock); "*Lopezia cylindrica* hort. bot. Paris, Bonpland" (G); Cult. in Serre, à la Pierrière, February 19, 1901, Beauverd (G); *L. coronata*, cult. in Berlin, July 1838, herb. Maire (P).

Lopezia racemosa subsp. *racemosa* is variable in almost every character, particularly in the following:

1. *Pubescence*: From densely hirsute or densely strigulose (long to short hairs, respectively) to subglabrous. Perennials are more variable than the annuals in this respect. The hairs can be erect or appressed, varying in color (whitish or rusty to purplish); some are glandular in some plants ("*L. glandulosa*"). The extent of hairiness often changes in an individual from season to season, and it frequently segregates in the progeny. Thus one can observe plants with glabrous or strigulose main stems and hirsute branches, and vice versa, or parental pubescent or subglabrous plants of which the progeny is only partly so. Very generally we can state that the most densely pubescent type is common in the south, whereas glabrescent or short-pubescent ones are more common in the north.

2. *Leaves*: As in most taxa of *Lopezia* the leaves are variable in size, shape, pubescence and serration—in individual plants as well as within and between populations—as implied in the general description. Material with relatively narrow leaves has often been determined as *L. angustifolia* or *L. lineata*. The leaves can be remotely spaced or dense ("*L. foliosa*"), persistent or early deciduous, correlated with the habit which, in turn is dependent, at least in part, on the ecological situation. The leaves are generally alternate though the lower ones and those on late branches are \pm opposite ("*L. oppositifolia*"); in the related *L. conjugens* they are mostly opposite. The dentation is less pronounced in the upper leaves, and it sometimes differs from plant to plant or from population to population. The teeth can be few and remote or dense and numerous, small to large, acute to shallow ("*L. integrifolia*"). Individual and population variation is also indicated in the number of lateral veins per leaf. The petioles are variable in length (0.15–4 cm); those of the upper leaves and bracts are shorter. Long-petioled leaves are more common among the annual and/or subglabrous plants, which tend to have subangular stems.

3. *Inflorescence*: The racemes are many or few per plant, short (ca. 5 cm) to rather long (30 cm or even longer), simple or branched and then forming an open panicle or infrequently a corymbose inflorescence ("*L. corymbosa*"), leafy below ("*L. axillaris*") to hardly so. The bracts are as variable as the leaves. The pedicels vary in length (0.6–2.7 cm), in color, pubescence and inclination; they are ascending to erect or sometimes curved in flower, drooping to ascending in fruit.

4. *Flowers*: Usually there are many, usually crowded at tip, more remote below. Certain populations have few-flowered or loose racemes. The flowering rate on a single plant as well as the whole pattern of phenology show wide variation; from very gradual and/or long flowering to an almost simultaneous and/or rapid flowering, once to two or three times during the year, and from midsummer

(July) to winter or early spring. Occasional plants or populations may even flower in June.

5. *Sepals*: Variable in size, pubescence and color, and—to a lesser extent—in shape and position (usually the upper three are straight, ascending, and close to each other but sometimes they are more divaricate). The length ranges from 3.5–7 mm.

6. *Petals*: Almost as variable as the leaves. The petals vary in color, size, shape and relative position. Their color ranges from pinkish-lilac or pink to red or purplish; in Chiapas orange-flowered plants are rather common (as in subsp. *moelchenensis*). White-flowered individuals have been observed also ("*L. albiflora*" and *Breedlove* 8030). Though the variation in color is \pm continuous there are two predominant forms: a) petals pinkish-lilac; these plants are often less hirsute and accordingly commoner in the north (referred to *L. racemosa* s. str. and *L. coronata*). b) Petals red (salmon or coral or purplish); often more hairy and commoner in the south (referred to *L. hirsuta* and *L. angustifolia* sensu Munz, 1961). Plants of these two sorts occur together in many of the recorded localities, and they often segregate from the progeny of a single individual. There is no evident biological barrier between them. In Guatemala, however, only red-flowered plants have been found. The variation in color parallels that of *L. miniata*; so does the variation in size of the petals, particularly the lower; their shape is also variable, even more so than in *L. miniata*. The upper petals are usually erect, but the lower may be almost divaricate or ascending to almost erect; sometimes they are ascending-divaricate with blades bent upward (then the blades are asymmetrically acuminate). The claws vary in length to a lesser extent; those of the upper petals are glabrous to distinctly ciliate-hairy. The blades are either of a single color or differ in shade in certain parts; bicolored petals are especially frequent among the pinkish-lilac type.

7. *Glands and auricles*: The upper petals lack true auricles; they are, however, slightly to conspicuously dilated at the base of the blade, above or around the gland, and sometimes even have short and obsolete, rounded auricles (but never well-developed ones like those of *L. miniata*). The glands vary in size (minute to rather large) and shape; they are usually round, but oblate or kidney-shaped ones on the one hand and ovoid or oblong ones on the other have been observed in several different populations.

8. *Fertile stamen and style*: Both vary considerably in length. The anther is variable to some extent in size and color. The pollen is mostly 3-pored, infrequently with a few 4-pored grains, which are frequent in subsp. *moelchenensis*.

9. *Staminode*: Much like the petals, the staminode varies in size and color. It might be also of the same color as the petals or of a different (paler or stronger) shade.

10. *Capsules*: Amply variable in size, less so in shape and inclination. Their dimensions range from very small, as in *L. miniata*, to very large, almost as large as in *L. trichota*. The latter are common in the sort of plants that have been called *L. coronata*. In many cases the capsules differ in size during the flowering season with the first ones usually the largest; this is partly true also for the flowers. In cultivation (or in the wild, under favorable conditions of moisture)

the capsules become on the average larger than normal. The shape is generally globose, yet plants with ovoid or oblong-ellipsoid, sometimes asymmetrical, capsules are not uncommon. There are many peculiar forms as well: obpyriform and subclavate (resembling those of *L. conjugens*), compressed at apex and apple-shaped, and ovoid-oblong or elliptic-obovoid (especially in subsp. *moelchenensis*). Certain extreme forms are explicitly recorded later. As to their inclination, the capsules either remain erect or ascending or bend into a nodding position.

11. *Seeds*: Variable in number per capsule (ca. 2–4 seeds per locule) as well as in dimensions; almost as a rule, the bigger the capsule, the more seeds (and larger ones) it contains. Some variability is pronounced in the texture of the seeds (*i.e.* size, shape and arrangement of the tubercles).

12. *Habit*: *Lopezia racemosa* includes annual and perennial strains, differing neither morphologically nor biologically and displaying almost the same wide variation. Either can be erect or ascending, procumbent or straggling. The stems vary from thick and woody to slender and herbaceous, in color (green or brownish to purple-red, in different or the same plants), in number and amount of branching; they are usually terete but sometimes (particularly in the annuals) \pm angular, rigid and straight to flexible. The branches are equally variable.

Plants and populations vary in their stature; small or delicate (*e.g.* “*L. annua*,” “*L. elegans*,” “*L. parvula*”) *vs.* huge and lush ones; stem length ranges from 10 cm or rarely less to 120 cm or even more. In several cases this variation, though genetically controlled, is obviously correlated with the habitat-conditions and changes accordingly.

Collections with many rooting stems are, among others: *Balls 5446*, *Moore 2401*, *H. Johnson 41*, *Raven & Breedlove 19806* and those of *Leavenworth*, and this habit is characteristic of subsp. *moelchenensis*.

Collections with peculiar pubescence are, among others: *Feddema 2802* from Guerrero (hirsute with partly purplish hairs, also glandular-pubescent); *Dodds 97* from Veracruz (with long-hirsute pedicels!); *Arsène* in 18.11.1909, from Michoacán (with long stiff hairs, some apparently glandular); *Flores C. 150* from Morelos (with densely and distinctly glandular-pubescent pedicels); *Rudd 2012* from Puebla (hirsute and glandulose-pubescent).

Collections with deeply and acutely serrate leaves are, among others, from Puebla (*Rose & Hay 5654*), Nuevo León, Hidalgo, México, Morelos (*Langman 2672A*), Michoacán (*Hinton 13281*), and Chiapas.

Many collections have short-petioled leaves (especially in perennials) or short-pedicelled flowers. Large, long-petioled leaves (which are probably the first ones) are common in the less hairy, angularly stemmed plants, which are frequently annual. Collections with corymbose racemes are mainly from Guatemala (*Heyde & Lux 2948*; *Naxon & Hay 3570*; *Bell & Duke 16965*); plants with leafy racemes, however, have been collected in several places throughout Guatemala and also in Chiapas. Specimens with exceptionally long pedicels are uncommon (*Abarca 67* from Teneria, México; *Bourgeau 1603* from the valley of Córdoba, Veracruz).

Collections with long racemes and/or large flowers (wide and long petals) are, among others: *Paray* 1283, *Pringle* 13988, *Rose & Painter* 7240, all from Morelos; *Abarca* 67, *Hinton* 7236, from México; *Bourgeau* 1603 from Veracruz; *Conzatti* 4858 from Oaxaca; *Shilom Ton* 505, *Breedlove* 7155, from Chiapas; also from Michoacán and Guatemala.

One collection, *Breedlove* 8030 from Oaxaca, consists of plants with completely white flowers. Many collections, particularly from Veracruz and México, are characterized by relatively small flowers and/or capsules. Some of these morphs represent distinct populations, each with its extreme traits, most of them located either in the northern part of the range (Durango, San Luis Potosí, Aguascalientes) or the eastern parts (Veracruz, Puebla, Hidalgo, and even Morelos). In addition to the ones we have singled out for discussion, there are many other forms, unique or distinguished in other traits, such as petal width, length and ciliation of claws, pedicel inclination, seed surface, and stem morphology. Certain populations might actually be regarded as microspecies, and a few (*Soderstrom* 875, *Paray* 3203) are probably new taxa. In a few cases more material is needed for a definite evaluation; in a few others their status is yet to be experimentally determined. Altogether, it seems that most belong or are related closely to *L. racemosa* sens. lat., as a superspecies (or macrospecies).

In our greenhouse experiments we observed the occurrence of certain physiological and other strains: Strains differing considerably in the degree of self-pollination; early flowering vs. late flowering plants; different germination and growth-rates; cold-resistant strains; strains consisting of plants with two flower colors (lilac and red-pink, *Breedlove* 8024); and plants with peculiar tomato-shaped capsules (*Breedlove* 9882). These and other cryptic strains taken together add to the remarkable polymorphism of the species.

Lopezia racemosa subsp. *racemosa* is very flexible in its reproductive biology. For example, all populations have the "snapping mechanism" for pollination in spite of the fact that some of them are ultimately highly self-pollinated; moreover, the plants occasionally propagate vegetatively by adventitious roots, as in subsp. *moelchenensis*. Teratological forms have been observed as well, both in the greenhouse or in wild material, especially from Veracruz. As a rule, these forms are fasciated and sometimes their reproductive parts (racemes, sepals, etc.) have become vegetative ones (e.g. *Botteri* 519 *pro parte*). A doubling of petals has also been noticed in some hybrids.

In addition to the wide genetic variability in *L. racemosa* subsp. *racemosa* is its rather extreme phenotypic plasticity, particularly in response to density (habit and flowering), moisture conditions (stature, pubescence, flowering) and temperature. Such plasticity, pronounced in almost every part or stage, is typical for weedy plants (usually annuals). The variation of *L. racemosa* is therefore in accordance with its ecological requirements. This species is rather an ubiquist, occupying primary and secondary habitats, on various soils, and in different climatic conditions as reflected by its large distribution. Its variability, polymorphism, and polytypy are consistent with those of eurochoric species. *Lopezia racemosa* subsp. *racemosa* is often a colonizer, invading cultivated or disturbed lands from its neighboring natural habitats. As in many other groups of plants,

it may have been through this process that annuality became prevalent in the population.

In view of the high degree of variability in *Lopezia racemosa*, its taxonomic complexity is not unexpected. Earlier in this century, Rose (1909) and Sprague and Riley (1924) divided not only it but also *L. miniata* into a number of species. By 1961, Munz had reduced these to only four: *L. racemosa* s. str., *L. hirsuta*, *L. angustifolia*, and *L. coronata*. The delimitation of these taxa, however, is based upon various inconstant, variable and uncorrelated characters (*e.g.* dimensions of flowers and capsules). Several plants or populations do indeed fit into the typical diagnoses, which is why taxonomists, with the scanty material they had and little biological information, treated them separately; many other populations are intermediate between these morphological modes. Munz (1961: 87–88) was already aware of this problem, listing certain “plants suggesting hybridity with *L. mexicana* and *L. angustifolia*,” and pointing out that some forms of *L. racemosa* approach *L. hirsuta* “with which it may well hybridize.” Though we consider all four units as one species, it is relevant to discuss them briefly one by one.

Lopezia racemosa s. str. is still the most variable taxon, which includes most of the synonymous specific units. This “species” is common in the state of México and characterized as follows: Annuals, pubescent to glabrescent; stems rather coarse, angular, usually branched; leaves ovate or broadly lanceolate; racemes simple or paniculate; pedicels \pm glandular-pubescent, ascending to reflexed (pending), axillary in bracts; upper petals linear or linear-oblong, obtuse; lower petals long-clawed, spatulate; capsule globose, 3.5–4.5 mm in diameter.

The original descriptions of *L. racemosa* and *L. mexicana* are quite general, covering the whole group. Any other differentiating characters (*e.g.* habit or stature, number of veins on leaves, length of racemes, branching dimensions of floral parts) are rather imposed than natural. Some representative collections of typical “*racemosa*” are, for example: Pringle 6580, Purpus 1697, Munz 15055, Breedlove 7201, Rzedowski 23325, Rose & Painter 7277, Weaver 976, Sohns 571, Bourgeau 767. Most of the rest of the material combines certain traits of the other categories.

Plants of the sort that have been called *Lopezia hirsuta* are very common throughout Mexico, particularly in the southern states of Chiapas and Veracruz. They are characterized as follows: Mostly perennials; stems terete, suffruticose, hirsute; leaves ovate to lanceolate, hirsute-pubescent especially beneath, remotely or shallowly serrulate; racemes leafy at base; flowers of one color; capsule ca. 3 mm in diameter.

As discussed, pubescence, color of petals, size of capsule are not sufficient for species delimitation and actually many hirsute plants share some features with “*racemosa*” or “*angustifolia*.” Some collections of typical “*hirsuta*” are, for example: Pringle 2973, 8127, Rzedowski 7143, Galeotti 3034, Balls 5446, Hinton 15464, 11280, Purpus 1696, 6803, Rose & Painter 7240, Breedlove 7030, Nelson 1338, Conzatti 3854, Bernoulli 234, Standley 59882, 59386. There are many hirsute annuals as there are “*racemosa*” perennials; red petals of one color, however, are more frequent in perennial or hirsute plants.

Lopezia coronata is characterized as follows: Annuals, subglabrous to pubescent; stems long, simple; leaves broadly to narrowly lanceolate, glossy, serrate; petioles somewhat decurrent; racemes simple, leafy, crowded at tip; pedicels spreading to recurved in fruit; flowers axillary, a little large in all parts; petals redder at base, whiter at apex; staminode whitish; capsule up to 8 mm long and 6 mm wide, globose or ovoid to obovoid.

The original drawing and description are based upon "a plant in the conservatory of the Countess de Vandes"; *i.e.* on a cultivated plant. In addition, Andrews made the point that "*Lopezia coronata* is . . . of recent introduction." Munz noted as well that he had found relatively few herbarium specimens collected in the wild and that "the status of this plant has been and still remains somewhat doubtful. In cultivation for about a century and one-half, it seems quite distinct from *L. racemosa*. . . ." We do agree that it is a form different from many others, yet in our opinion it is simply a cultivar of *L. racemosa*. The wild material cited by Munz (*Wawra* 950, *Standley* 22804, 22876, *Purpus* 6805) is either *L. racemosa* subsp. *racemosa* or *L. racemosa* subsp. *moelchenensis*. This cultivar was introduced in many European botanical gardens as early as 1805 (Aiton, 1810, vol. 1, p. 10). *Lopezia racemosa* had been introduced into botanical gardens in 1791 and was widespread in cultivation by 1796. Andrews, unaware of the variability and polymorphism in that group, regarded *L. coronata* as a distinct species.

Apart from *Lopezia coronata* there are a few other cultivars, one of which is *L. lineata* Zucc., which in habit is intermediate between *L. racemosa* and *L. angustifolia*: hirsute-pubescent, with small upper leaves, glabrous pedicels but somewhat pilose sepals, petals violet-white. Plants of this sort have been in cultivation since about 1837. Zuccarini based his diagnosis and observations on plants grown from seeds taken from Karwinski's Mexican collection. He drew the distinctions between this taxon and the related ones (*L. racemosa*, including *L. coronata* and *L. hirsuta* or "*L. tuberosa*"), distinctions which we now consider insignificant.

Another cultivar is *Lopezia cordata* Hornem., which according to the author was introduced into cultivation 1813 and is distinguished from *L. racemosa* by having some subrotund-ovate-cordate leaves and purple flowers, plus a few minor traits. Undoubtedly this taxon is synonymous with *L. racemosa*.

Lopezia minima Lag. ex Schrank is also known from cultivation, together with *L. coronata*, and they are apparently identical. Many plants of *L. racemosa* s. str. display certain characteristics of *L. coronata*; typical collections of the latter, all of cultivated specimens, are for example: *Lopezia coronata*, herb. Fenzl (W), herb. M. E. Moricand (G), herb. Gadeceau (BM), ex horto bot. Petropolitano (US), from hort. Copenhagen (S), herb. H. Van Heurck (P), herb. Tho. Clark (K), *Lopezia coronata* Andr. and *L. axillaris* Thunb., from H. Ups. (S), and from Bern in 1927, Meisner herb. (NY).

Lopezia angustifolia is characterized as follows: Shortly pubescent to glabrescent perennials; stems \pm angular and purplish, branched; leaves narrowly lanceolate or oblanceolate to linear, shorter than usual, the upper ones a little

smaller, narrow; petioles short; petals purplish, the upper with a broad gland; capsules oblong-ovoid; inflorescence branched, racemes many.

The type collection (*Pringle 3990*) is closer to *L. racemosa* s. str. than to *L. hirsuta*, and in some respects (stems, capsules) it resembles *L. nuevo-leonis*. There are only a few similar collections, mostly from San Luis Potosí (*Palmer 159*, type of *L. elegans*), and probably these are populations typical of and limited to that part of Mexico. Subsequent to the original description, Munz (1961) unjustifiably broadened the description, emended it, and included plants of the sort that have been called *L. foliosa* in *L. angustifolia*. Except for the branched habit, the narrower leaves, and probably the somewhat smaller flowers there is no evident similarity between these two taxa. *Lopezia foliosa* is more related to "*L. hirsuta*," by such features as its hirsute to pubescent habit, subterete and rooting stems, and small capsules. It is distinguished by its smaller leaves, shallowly serrate to entire, shorter floral parts and densely leafy branches. Populations of this kind, though less leafy and more hirsute, are common in the state of Veracruz, but they are also found in Guerrero, Oaxaca, Chiapas, and Guatemala. Accordingly, most of the specimens cited by Munz are not true *L. angustifolia*, due to his misconception of this taxon; they resemble \pm the *foliosa*- or Veracruz-type. Several other collections, from various places, are transitional between *L. foliosa* and typical *L. hirsuta*. Collections of *L. foliosa* (or *L. angustifolia* sensu Munz) are, for example: *Purpus 7076*, *Bilimek 961 p.p.*, *Muller (1524)*, *Bourgeau 3226*, *Miranda 650*, *4882*, *Gómez Pompa 1824*, from Veracruz; *Conzatti 4858*, *Galeotti 3060*, from Oaxaca; *Tillett 638-80*, from Chiapas; *Pittier 20*, from Guatemala. Partly so are: *Schiede & Deepe 535*, *Rose & Hay 6148*, *Pringle 8127*, *Seaton 132*, *Balls 4278*, *Conzatti & Gonzáles 1115*, *White 5058*, *Fisher 342*, *C. L. Smith 1786*.

On the other hand certain specimens are intermediate between the true, typical *L. angustifolia* and *L. racemosa* s. str. usually with small capsules; among them: *Palmer 256 1/2 p.p.*, *Rzedowski 8110*, from San Luis Potosí; *Palmer 839*, *Ripley & Barneby 13503*, from Durango; *Ripley & Barneby 13365*, from Guanajuato; *L. parvula* (*Nelson 4987*, from Durango) and *L. lineata* (cultivated, e.g. *Raven 11404*) as well as certain collections from Hidalgo might be partly included in this category.

The four species recognized by Munz (1961) and discussed above thus not only intergrade extensively, but they represent particular combinations of characteristics not necessarily representative of entire populations. Furthermore, there are a number of other morphological types within the subspecies that might equally warrant taxonomic recognition, if there were any indication that such recognition would be an aid to understanding the extremely complex pattern of variability in this extraordinary taxon. Among these extreme types are the following:

1. Shrubby plants with leaves partly opposite or clustered; sepals or petals long; anther ca. 2 mm long; petals not auricled; capsules rather large: El Salvador, Volcán San Salvador, *Williams & Molina 15103* (GH); Guatemala, mts. near Hacienda of Chaucol, *E. W. Nelson 3659* (GH, US). A rather similar plant with

proportionally wide and shallowly serrate leaves and claws of upper petals long-ciliate is *Williams, Molina & Williams 25341* (DS) from Lake Atitlán, Guatemala.

2. Branched annuals; racemes long and many-fruited; flowers small and short-pedicelled; lower petals relatively narrow; capsule minute, 2.5–3.5 mm long: Durango, *Palmer 839* (BM, GH, K, MICH, MO, NY, S, UC, US). Somewhat similar plants, with oblong-lanceolate to lanceolate-linear early deciduous leaves and narrow pale-bright petals, have been seen from 19 mi. SW of Durango, *Ripley & Barneby 13503* (DS, NY).

3. Capsules obpyriform, constricted at base; seeds oblong-ovoid: Michoacán, Coalcomán, Sierra Torrecillas, *Hinton et al. 15264 p.p.* (G, GH, MICH, NY, UC). Other collections with such capsules are *Orcutt (4253)* in 3.10.1910, from Xochimilco, Distrito Federal (BM, MO), *Smyth 205* from San Angel, Distrito Federal (US), *Muller 1573* from Vera Cruz to Orizaba (K), and *Rzedowski 23560* from S of Amojileca, Guerrero (IPN).

4. Delicate perennials (or annuals); stems appressed-pubescent, upper leaves somewhat so; leaves narrower than 1.1 cm, remotely or shallowly serrate to almost entire; flowers small; petals subequal (!), 1.2–2 mm wide, oblong-oblongeolate to oblong-obovate, slightly denticulate-sinuate at apex, the upper obtusely and shortly auricled with a single kidney-shaped (!) gland; capsules 2–4 mm in diameter: Chihuahua, W side of sierras, near San Francisco del Oro, *Soderstrom 875* (MICH, US). These plants, out of the range of *L. racemosa* and with habitus and colors of *L. miniata*, might be either intergrades with the latter or an undescribed species.

5. Tiny plants, up to 9 cm tall; leaves to 1.2 × 0.6 cm, oblong-ovate to lanceolate-linear, remotely serrulate, alternate to opposite; branches and racemes very short; flowers minute, all parts shorter than 3 mm (!); petals hardly clawed, the upper without auricles or distinct glands: Hidalgo, Cerro Cangando, Encarnación, *Paray 3203* (IPN). These plants might be hybrid-segregates or ecotypes or even new species. There are many other small specimens (*e.g. Moore 1565* (BM, GH, MICH, UC) from Pachuca to Real del Monte, Hidalgo, with small, short-pedicelled capsules; *Dugés 308b* (GH) from Santa Rosa Mts. in Guanajuato, with simple stems and small capsules; *Rzedowski 19272* (IPN, MICH) from Ixtlán de Juárez, NE of Oaxaca, with capsules sometimes ellipsoid; *Beauchamp* in October 1926 (MO), from Amecameca, Mexico, with opposite leaves; *Coulter 179* (GH, K, NY) from Zimapan partly so; and likewise from Veracruz, Aguascalientes, San Luis Potosí and Michoacán) yet none is as unique as the ones mentioned above.

6. Generally like "*L. coronata*"; stems angular, slightly winged; leaves acutely serrate; racemes short and crowded; upper petals with a broad constricted or kidney-shaped gland; Nuevo León, Monterrey, canyon above El Diento, *R. F. Smith M575* (TEX). This plant shares some features with *L. nuevo-leonis*. Other specimens ± resembling this one, particularly in having this kind of gland, are recorded from Morelos, Lagunas de Zempoala, *Breedlove 15835* (DS), San Luis Potosí, Sierra de Álvarez, near Puerto Huerta, *Rzedowski 5269* (IPN), Guerrero, México, Oaxaca, Veracruz and Aguascalientes.

Some specimens of *L. racemosa* subsp. *racemosa* have certain features of *L. miniata* subsp. *miniata*, probably the result of convergent evolution rather than hybridization. Such plants have an unusually broad gland on the upper petal, sometimes with small auricles, mostly with small capsules, with long and branched inflorescence and sometimes with shallowly serrulate leaves (e.g. *Ch. L. Smith 844 p.p.* from Oaxaca; *McVaugh & Koelz 153* from Aguascalientes; *Langman 3057* from Michoacán, with small auricles and small glands). These species can be hybridized in the experimental garden, and *Rzedowski 8310* and *10001* might represent wild hybrids of this parentage.

14b. *Lopezia racemosa* subsp. *moelchenensis* Plitmann, Breedlove & Raven, subsp. nov.—FIGS. 76–79.

Herbae perennes subglabrae. *Caules* decumbentes ad erectae, strigulosae vel subglabrae, adnodos radicanes. *Folia* crassa, glabra, 0.7–4.4 cm longa, (0.1–)0.2–1.4 cm lata, anguste lanceolata vel rariore ovata vel oblanceolata, serrulata vel serrata. *Petala* carneo-aurantiaca ad rubra. *Pollen* saepe 4-porata interdum 3- vel 5-porata. Numerus chromosomaticus gameticus, $n = 20$.

Subglabrous perennial *herbs*. *Stems* mostly decumbent, sometimes erect, sparsely strigulose, or glabrous rooting at nodes. *Leaves* fleshy, glabrous, 0.7–4.4 cm long, (0.1–)0.2–1.4 cm wide, narrowly lanceolate, more rarely ovate or oblanceolate, acuminate or cuneate-angustate at base, serrulate or serrate, the teeth usually with dark clusters of “oil cells” (Stein, 1915) at the tips. *Pedicels* 1–3 cm long. *Petals* pink-orange to orange-red, sometimes pink-brown or tinged with lilac. *Pollen* with a high proportion of 4-porate and some 5-porate grains, in addition to the 3-porate ones typical of diploids. Gametic chromosome number, $n = 20$.

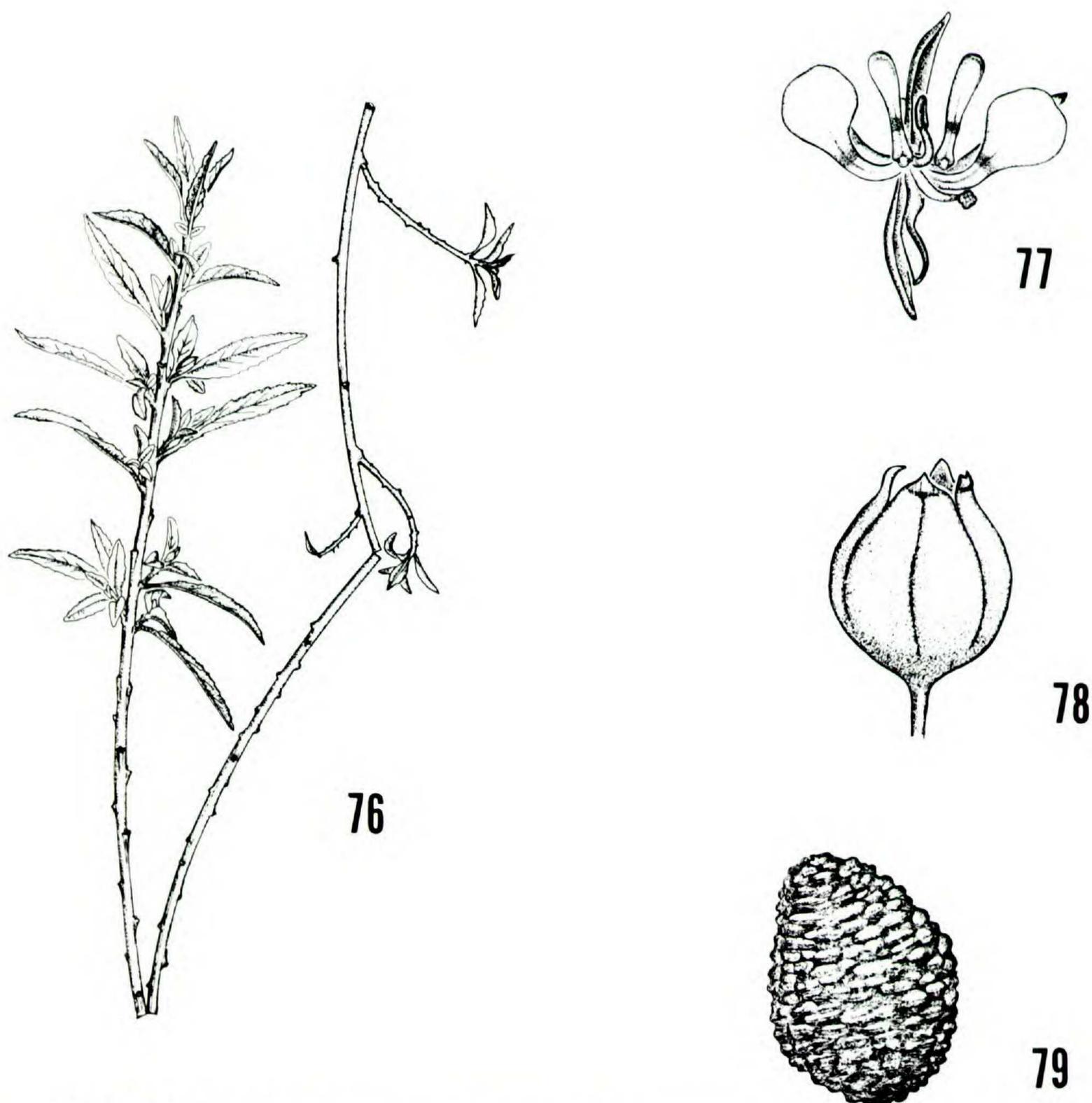
TYPE: Chiapas, Moel Ch'en near Tenejapa Center, Municipio of Tenejapa, 7500 feet, 30 November 1964, *D. E. Breedlove 7794* (DS).

Distribution (Fig. 66): Steep exposed limestone slopes with *Saurauia*, *Quercus*, and *Pinus* in Chiapas, Mexico, and probably northwestern Guatemala, 1800–2500 m elevation. Flowering, November to March but sporadically throughout the year.

Additional specimens examined:

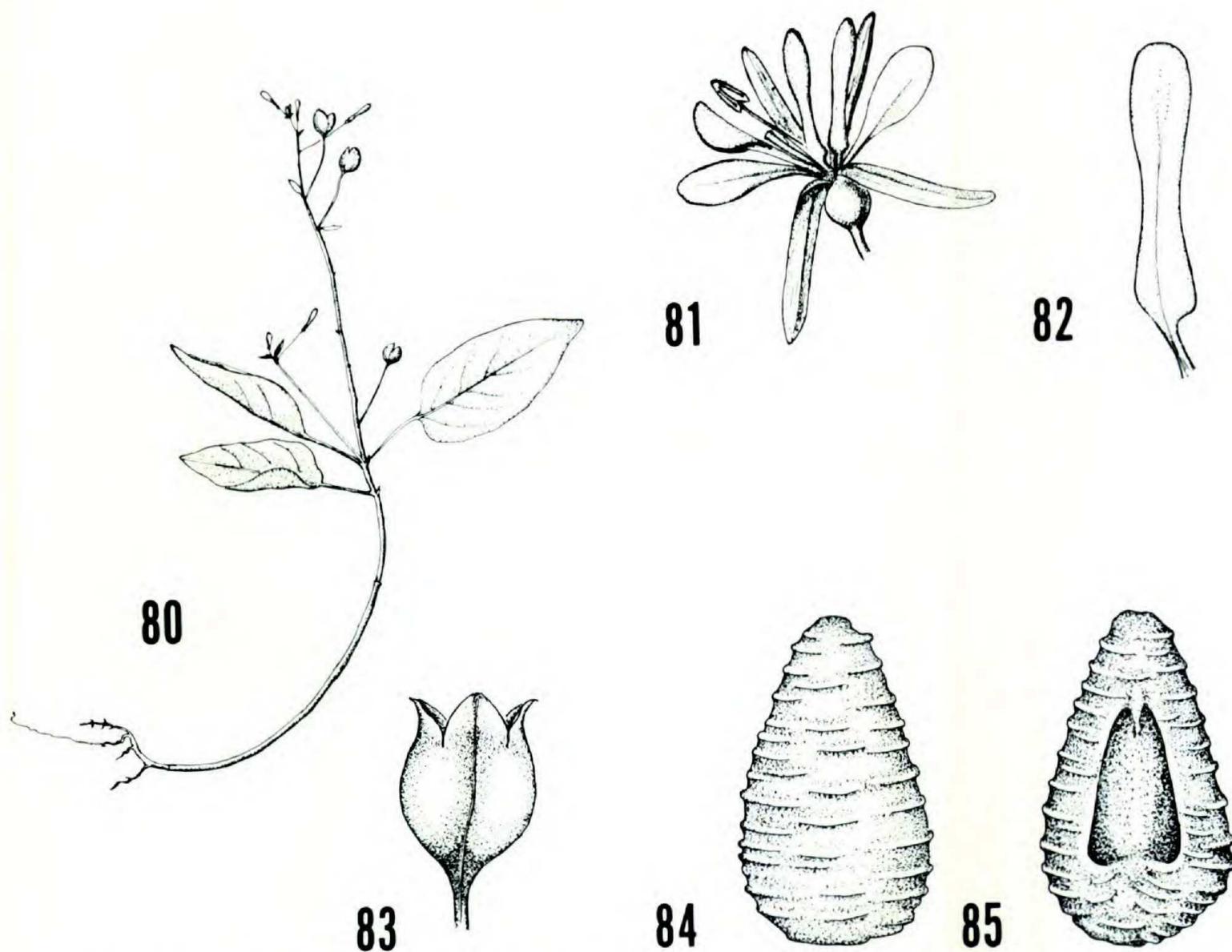
MEXICO. CHIAPAS: Chihk Ha', paraje of Yashanal, Tenejapa, *Breedlove 9373* (DS); near Tenejapa Center, *Breedlove 6971* (DS); Moel Ch'en near Tenejapa Center, *Breedlove 9343* (DS).

As stressed above, *Lopezia racemosa* subsp. *moelchenensis* is undoubtedly a tetraploid derivative of *L. racemosa* subsp. *racemosa*. Its variability is rather narrow and the various populations are more or less uniform morphologically. It grows exclusively in particular extreme microhabitats under conditions probably unfavorable for the sympatric subsp. *racemosa*. There are important biological distinctions between the two in chromosome number (which leads to a reduction in fertility of the hybrids), ecology, and flowering time (subsp. *moelchenensis* flowers later in the year than subsp. *racemosa*, although sporadically at other times also). These seem to have allowed the evolution of this narrowly restricted but distinctive entity, which might be regarded as a species “in statu nascendi.”



FIGURES 76-79. *Lopezia racemosa* subsp. *moelchenensis*.—76. Branch, $\times 0.59$.—77. Flower, $\times 2.3$.—78. Capsule, $\times 7$.—79. Seed, abaxial view, $\times 23$. All from progeny of the type collection, grown at Stanford University.

A peculiar single collection similar to *L. racemosa* subsp. *moelchenensis* is *Breedlove* 8688 (DS) from stony ledges of the Wahshaklahung Pyramid in San Mateo Ixtatán, Guatemala. The leaves of these plants, which likewise have a gametic chromosome number of $n = 20$, are less fleshy, generally wider and more sparsely hirsute than in subsp. *moelchenensis* from Chiapas; the petioles average longer (to 2 cm); the pedicels \pm puberulent-glandular; the petals a little larger; and the pollen grains mostly 3-porate. Plants of this sort have been found only in the Sierra de los Cuchumatanes and might constitute an independent tetraploid derivative of *L. racemosa* subsp. *racemosa* which needs to be studied further in the field. Another collection from the same area, *Breedlove* 8496 from 7 mi. S of San Juan Ixcoy along road to Huehuetenango, resembles both the collection from San Mateo Ixtatán and *L. racemosa* subsp. *racemosa* (larger somewhat pubescent leaves, long petioles, large flowers, \pm erect stems, etc.).



FIGURES 80–85. *Lopezia conjugens*.—80. Habit, 0.55.—81. Flower, $\times 2.8$.—82. Upper petal, $\times 3.3$.—83. Capsule, $\times 3.3$.—84. Seed, abaxial view, $\times 22$.—85. Seed, adaxial view, $\times 22$. All from the holotype.

15. *Lopezia conjugens* T. S. Brandege, Univ. Calif. Pub. Bot. 6: 59. 1914. Munz, Brittonia 13: 86. 1961; N. Amer. Fl. II. 5: 21. 1965.—Figs. 80–85.

Sparsely puberulent or subglabrous *annuals*. Stems 1–3.5 dm tall. *Leaves* 1–4.5(–5) cm long and (0.6–)1–3 cm wide, apparently mostly opposite, ovate, obtuse at base, acute at apex, thin, subglabrous, with 4–8 veins on each side of midrib, shallowly serrulate-crenulate to mostly subentire, remotely ciliolate-strigose; petioles 0.5–3 cm long, slender, usually narrowly winged. *Bracts* 2–10 mm long and 1–2 mm wide, mostly glabrous but slightly hairy toward apex; pedicels 8–17 mm long, spreading to ascending, minutely glandular-puberulent. *Sepals* ca. 5.5–7 mm long and 1–1.5 mm wide, oblong, subglabrous. *Lower petals* ca. 6–7 mm long and ca. 2 mm wide, obovate-spatulate or elliptic-ovate, angustate then clawed at base, obtuse at apex, purplish; upper petals ca. 6 mm long and ca. 1.5 mm wide, oblanceolate-oblong to linear, angustate into a short claw, without a conspicuous gland, obtuse at apex, pale-purplish. *Fertile stamen* ca. 5 mm long; anther ca. 1.5 mm long, purplish. *Staminode* ca. 6 mm long and ca. 3 mm wide, obovate-spatulate, narrowed at base, emarginate at apex, pale purplish. *Style* ca. 3–4.5 mm long; stigma minute. *Capsule* ca. 5 mm long and 4 mm wide, subglobose, slightly clavate-cuneate at base, glabrous. *Seeds* 1.2–1.5

mm long, oblong-ovoid, somewhat incurved, rugose with linear transverse tubercles, blackish-brown.

TYPE: Mexico, Sinaloa, Copradia (Cofradia), near Culiacán, 25 October 1904, T. S. Brandege (UC; isotype, GH).

Distribution (Fig. 66): A rare endemic of Sinaloa, Mexico. The type locality is now under water.

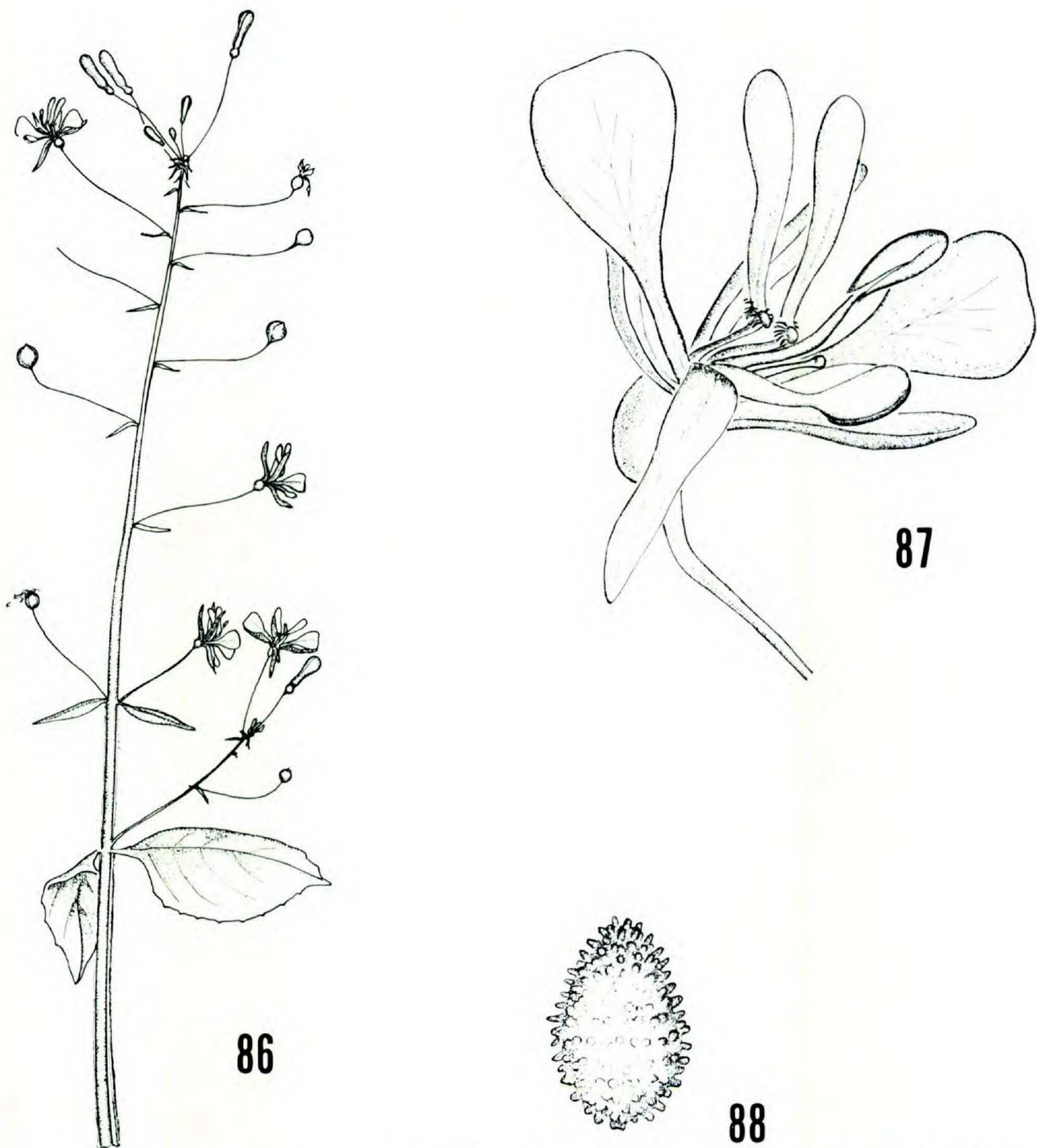
Like *Lopezia smithii*, the following species, *L. conjugens* seems to be an annual derivative of *L. racemosa*, which originated at the margin of distribution of the latter. It is known only from the type collection, which has few flowers and no ecological information.

Superficially *Lopezia conjugens* is very similar to *L. racemosa* but distinguished by certain significant traits: Leaves generally opposite, few-veined, shallowly serrulate to subentire; petioles usually narrowly winged; upper petals without a conspicuous gland; anther purple; seeds rugose with linear transverse tubercles, 1.2–1.5 mm long. Brandege's diagnosis is somewhat inaccurate in a few details: "Petalis superioris—margine infra medium plus minus glandulosis" already emended by Munz as "without conspicuous gland or turbercle"; "inferioribus late linearibus"—whereas they are actually elliptic- or spatulate-obovate. Perhaps Brandege misinterpreted the position of the flower, viewing the lower petals as upper ones and *vice versa*. In addition, the staminode is *not* minutely serrate; style and filament are a little *shorter* than petals, etc. Munz (1961: 86) described the capsule of *L. conjugens* as slightly clavate at base and uses this character in his key. Considering the wide variation of capsule-shape in *L. racemosa*, and since the clavation in *L. conjugens* is inconstant and slight, this character is not a useful one for separating them.

Brandege considered *L. conjugens* "intermediate between *Lopezia* proper and *L. clavata*," probably because of his misconception of the petal-position.

16. ***Lopezia smithii*** Rose, Contr. U. S. Natl. Herb. 12: 300, *fig. 46*. 1909. Munz, Brittonia 12: 85. 1961; N. Amer. Fl. II. 5: 21. 1965.—FIGS. 86–88.

Puberulent-strigose *annuals*. Stems 1–7 dm tall, angular and somewhat winged. Leaves ovate to lanceolate, the lower to 7 cm long and 2.8 cm wide, the upper 1–3.5 cm long and 0.3–1.5 cm wide, \pm cuneate at base with lower part gradually narrowed and somewhat constricted then with usually subparallel sides toward the base, acute at apex, shallowly serrulate, sparsely strigulose, with 5–12 veins on each side of midrib, subsessile. Bracts mostly 2–10 mm long and 0.5–4 mm wide, pedicels 10–19 mm long, patent to ascending, sparsely strigulose or puberulent to subglabrous. Sepals ca. 4 mm long and to 1 mm wide; sparsely strigulose or subglabrous. Petals pink-lilac to purplish-red; lower petals ca. 6 mm long and 2.5 mm wide, obovate, tapering at base into a claw as long or a little longer than blade, subentire and \pm retuse at apex; upper petals ca. 5 mm long and 1 mm wide, linear-oblong, not auricled, with claw shorter than blade and a single yellowish gland at base of blade fringed with marginal short, clavate hairs, retuse to obtuse at apex. Fertile stamen ca. 3–3.5 mm long; anther 1–1.5 mm long. Staminode 3–4 mm long, obovate, purplish, \pm emarginate at apex,



FIGURES 86–88. *Lopezia smithii*.—86. Inflorescence, $\times 0.58$.—87. Flower, $\times 7$.—88. Seed, abaxial view, $\times 23$. All from the holotype.

narrowed into a somewhat dilated and slightly ciliate-pubescent claw. *Style* 2.5–3.5 mm long, thin; stigma minute. *Capsule* 3–4.5 mm long, 2.5–3.5 mm thick, globose, rarely ellipsoid, open a third of its length, glabrous. *Seeds* ca. 1 mm long, oblong-ovoid, muricately and coarsely papillose-tuberclad, brown.

TYPE: Mexico, Oaxaca, Jayacatlán, 4300 feet, 4 November 1895, *C. L. Smith* 294 (US; isotype, GH).

Distribution (Fig. 66): Endemic in the mountains at the northeast end of the valley of Oaxaca, Mexico. Flowering, November and December.

Additional specimens examined:

MEXICO. OAXACA: Mountains, San Juan del Estado, *C. L. Smith* 427 (GH, US).

Collected only twice, by C. L. Smith, from neighboring localities, *Lopezia smithii* is probably an annual derivative of *L. racemosa*. Unfortunately, nothing is known about its habitat or its chromosome number. This species is easily distinguished by its slightly winged stems, subsessile leaves with unique base, \pm retuse petals, and the clavate hairs at base of the upper petals and around the glands. In other respects, it resembles *L. racemosa*.

Section V. *Nannolopezia*

Lopezia sect. *Nannolopezia* Plitmann, Raven & Breedlove, sect. nov.

Herbae tenues annuae. *Folia* alternantia, integra. *Inflorescentia* terminalia, racemosa. *Flores* purpurei albique, autogami, partibus libris. *Sepala* subaequalia. *Petala* alba, superiora quam inferiores angustiora, 1-glandulosa. *Stamen inferiorum* infertile; stamen superiorum tortum vel intortum. *Pollen* caeruleum. *Capsula* subglobosa. *Semina* 4, tuberculata, papillis parvibus longitudinalibus. Numerus chromosomaticus gameticus, $n = 7$.

Slender stemmed annual *herbs*. *Leaves* alternate, entire. *Inflorescence* terminal, racemose. *Flowers* purplish and white, autogamous, the parts free. *Sepals* subequal, often reddish. *Petals* white, the upper ones somewhat narrower than the lower ones, 1-glanded. *Upper stamen* fertile, the lower one petaloid but not clasping the fertile one; upper end of filament of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position, or not, in any case shedding pollen directly upon the simultaneously maturing stigma. *Pollen* blue. *Capsule* small, subglobose, the valves splitting for about a third of their length. *Seeds* one per locule, longitudinally papillose-tuberculate. Gametic chromosome number, $n = 7$.

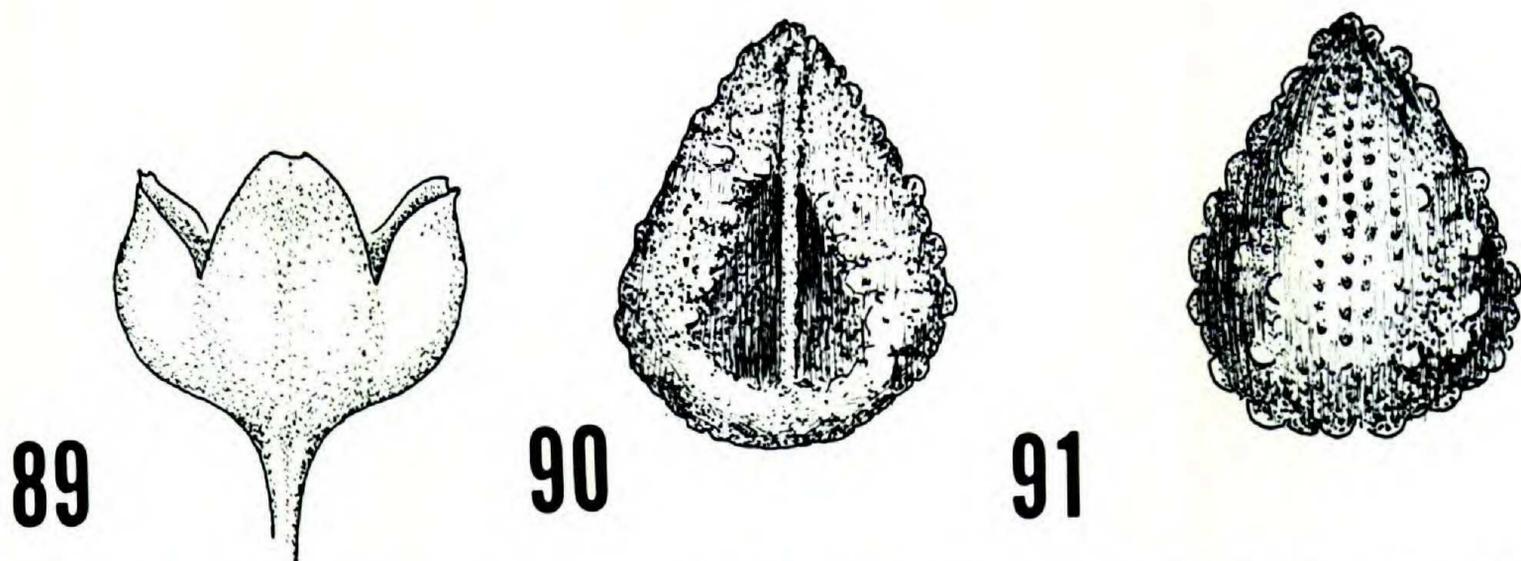
TYPE SPECIES: *Lopezia gracilis* S. Wats.

Distribution: Pine-oak forests of the Sierra Madre Occidental of Sonora, Chihuahua, and northern Durango, Mexico, 1700–2700(–3000) m elevation.

For a time, we considered this morphologically and chromosomally distinct species as a probable derivative of sect. *Lopezia*; there is, however, no evidence that it was in fact derived from a species in which the snapping mechanism of the fertile anther and staminode was present, especially in view of the somewhat distinctive anatomical features discussed by Eyde and Morgan (1973). We now regard it as derived from the ancestors of the evolutionary line that later gave rise to sect. *Pelozia*, but before the fusion of floral parts that is characteristic of this line had appeared.

17. ***Lopezia gracilis*** S. Wats., Proc. Amer. Acad. Arts 21: 429. 1886. Munz, Brittonia 13: 84. 1961; N. Amer. Fl. II. 5: 20. 1965.—FIGS. 89–91.

Delicate subglabrous *annuals*. *Stems* 1–3.5 dm tall, ascending to erect, usually branched, thin and slender, terete. *Leaves* 0.4–2.9 cm long and 0.1–1 cm wide, broadly lanceolate or oblanceolate to linear, usually narrow, obtuse to cuneate at base, subacute at apex, entire; petioles 0–0.8 cm long. *Bracts* narrow, linear to filiform; pedicels 7–15 mm long, ascending or spreading. *Sepals* 2–4 mm long and ca. 1 mm wide, glabrous. *Lower petals* (2.5–)3–4.5 mm long and 2–3 mm wide, obovate-suborbicular, obtuse, angustate then short-clawed, white; upper petals (2.5–)3–5 mm long and 1.2–2.2 mm wide, oblong, subacute to obtuse, obtuse-



FIGURES 89–91. *Lopezia gracilis*.—89. Capsule, $\times 11$.—90. Seed, adaxial view, $\times 36$.—91. Seed, abaxial view, $\times 36$. All from Gentry 635 (DS).

truncate to subcordate at base of blade, short-clawed, white with a broad green gland and a red blotch or band above it. *Fertile stamen* ca. 2.5 mm long; anther ca. 0.7 mm long. *Staminode* 2–3 mm long, obovate-obcordate, angustate-clawed below blade but a little dilated (like filament) at base, white. *Style* 2–3 mm long; stigma 0.5–0.7 mm in diameter, white; ovary obovoid-subglobose. *Capsule* 1.5–3 mm long, 1.5–3 mm thick, subglobose, subangular; valves ovate, somewhat wrinkled, \pm recurved and sometimes dark at the slightly emarginate apex. *Seeds* 1–1.5 mm long, ca. 0.8 mm thick, ovoid or obovoid, longitudinally papillate-tuberculate, dark brown. Gametic chromosome number, $n = 7$.

TYPE: Mexico, Chihuahua, Cumbre, above Batopilas, October 1885, *E. Palmer* 337 (GH; isotypes, BM, MEXU, NY, US).

Distribution (Fig. 34): Sandy creek banks and open places in pine-oak forests of the Sierra Madre Occidental of Sonora, Sinaloa, Chihuahua, and northernmost Durango, Mexico, 1700–2700(–3000) m elevation. Flowering, August to October.

Representative specimens examined:

MEXICO. SONORA: El Campanera, 41 mi. NE of Nuri, *Dunn* 9101 (RSA); El Rancho del Roble, NE of El Tigre, *White* 4314 (MICH); El Bilito, NE of El Tigre, *White* 4779 (GH, MICH); Cananea, Municipio de Yecora, *Donnelly* 48 (UC); El Tigre Canyon, E of Esqueda and Lago Angostura, *Turner et al.* 2105 (DS, MEXU). **CHIHUAHUA:** 10 mi. N of Madera along rd to Chuhuichupa, *Breedlove* 15535 (DS); Santo Domingo on Matachic-Ocampo, *Hewitt* 81 (GH); Cañon Huahuatán, SE of Madera, *Müller* 3442 (GH, US); Sierra Madre, SE of Colonia Garcia, *Townsend & Barber* 281 (BM, G, GH, K, MO, NY, P, US, Z); Sierra de las Papas, *Gentry* 635M (DS, MICH); Memelichi, Río Mayo, *Gentry* 2749 (GH, MEXU, MO, S, UC, US); Sierra Gazachic, 35 km SW of Miñaca, *Pennell* 18880 (MEXU, NY, US); base of Cerro Mohinora, 8 mi. from Guadalupe y Calvo, *Nelson* 4834 (GH, US), *Pennell* 18976 (US). **SINALOA:** 5 mi. E of La Cienega, Sierra Surutato, *Breedlove & Thorne* 18563 (CAS, DS, RSA). **DURANGO:** Hidalgo del Parral to El Vergel, 11.5 mi. W of Ojito, *Reveal & Hess* 3034 (US).

Sereno Watson (1886: 429) accurately listed the main distinctions between *Lopezia gracilis* and *L. cornuta*. These species occur sympatrically in the southern parts of the range of *L. gracilis*, but *L. cornuta* apparently grows in moister places. These two species show homologous variability in many traits. *Lopezia gracilis* has small white flowers and is highly self-pollinated; insects very rarely visit its flowers. Its stamen is not always completely twisted, and it can shed the pollen on the stigma just below it.

Section VI. *Pelozia*

Lopezia sect. *Pelozia* (Rose) Plitmann, Raven & Breedlove, comb. nov.

Pelozia Rose, Contr. U. S. Natl. Herb. 12: 295. 1909.

Well branched annual *herbs* or stoloniferous *perennials*. *Stems* often reddish. *Leaves* alternate. *Inflorescence* terminal, racemose, leafy, often reddish. *Flowers* pinkish or lilac to red or purplish, often with white markings, extremely zygomorphic, protandrous or autogamous, the constriction separating perianth, style, and androecium from the ovary prolonged into a neck. *Flower* parts except the staminode and lower sepal greatly displaced to upper side of flower, the three upper sepals and two upper petals united near the base, with the median upper sepal bearing a prominent gland at approximately the level of divergence and the two upper petals bearing less prominent or obsolete glands at this level; upper petals \pm equal to or much larger than the lower ones. *Sepals* often reddish. *Style* and *fertile stamen* united to one another and to the other upper floral parts near the base, but diverging well below the level of separation of the upper petals; upper stamen fertile, the lower one petaloid but not clasping the fertile one; upper end of fertile stamen rotating 180° at maturity, so that the basically introrse anther becomes extrorse in position. In protandrous species, fertile stamen reflexes downward after shedding its pollen while style elongates to occupy its former position. *Pollen* blue or yellow. *Capsule* ovoid to subglobose or clavate-obconical or subcylindrical, widely open at maturity or the valves opening at the very apex only, often reddish. *Seeds* many, small, finely tuberculate. Gametic chromosome numbers, $n = 10, 9, 7$.

TYPE SPECIES: *Lopezia laciniata* (Rose) M. E. Jones.

Distribution: Mexico, from southern Baja California and Sinaloa south in the Sierra Madre Occidental to Durango and Jalisco, in oak-pine forest or subtropical thorn shrub, 100–2000 m elevation.

18. ***Lopezia lanciniata*** (Rose) Jones, Contr. West. Bot. 15: 147. 1929. Munz, Brittonia 13: 83. 1961; N. Amer. Fl. II. 5: 20. 1965.

Pelozia laciniata Rose, Contr. U. S. Natl. Herb. 12: 296, fig. 38. 1909.

Generally subglabrous perennial *herbs*. *Stems* 1–6 dm tall, decumbent to erect, hirtellous, especially at base, to subglabrous; branches slender, glabrescent. *Leaves* thick, 0.7–5 cm long and 0.2–2.2 cm wide, the lower ones ovate to oblong or lanceolate, subcordate to obtuse or tapering to cuneate at base, acute or acuminate at apex, remotely serrate or serrulate, sparsely strigulose-hirtellous to subglabrous, upper leaves smaller, oblong to narrowly lanceolate, obtuse to acute-cuneate at base, acute at apex, subserrate to subentire, subglabrous, all with 0–5 veins on each side of midrib; petioles (1–)2–23(–29) mm long, subglabrous. *Bracts* 5–25 mm long and 1–6 mm wide, subglabrous; pedicels 15–45(–50) mm long, ascending to erect, sparingly glandular-puberulent to subglabrous. *Flowers* protandrous. *Sepals* 3.5–7 mm long and 1–1.5 mm wide, a few hairs present at apex, otherwise subglabrous. *Petals* white with red veins; lower petals 4–6.5 mm long and 1.5–2 mm wide, linear-oblong, sessile, subacute

and subentire at apex, sometimes retuse-bidentate, with subentire margins; upper petals 4–6.5 mm long and 3–4.5 mm wide, obovate-obtriangular, bipartite and shortly (3–)4(–5)–laciniate, somewhat clawed, adnate at base to upper sepals \pm dentate or incised at apex, sparsely serrate. *Fertile stamen* 3–5 mm long; anther 1–2 mm long, red. *Pollen* blue. *Staminode* 2.5–4.5 mm long, linear, plane or concave, white with red markings. *Style* 3–4.5 mm long; stigma 1–1.5 mm in diameter, whitish or lilac; ovary 1.5–2.5 mm long, obovoid-ellipsoid, \pm glandular-puberulent. capsule 2–5 mm long, 2–4 mm thick, obovoid-obconical, cuneate at base, truncate and dentate at apex, puberulent or subglabrous; valves open widely to about a third of their length. *Seeds* 0.5–0.9 mm long, ovoid, somewhat compressed, blackish. Gametic chromosome number, $n = 10$.

Distribution (Fig. 20): Moist seepages, especially along cliffs and in rocky places, in the Sierra Madre Occidental, in Mexico, (800–)1300–2800 m elevation. Flowering, October to February (March).

KEY TO THE SUBSPECIES

Stems short-hirsute; leaves narrowly lanceolate to lanceolate, all narrower than 1 cm, the upper ones very shortly petiolate 18a. subsp. *laciniata*
 Stems subglabrous; leaves ovate to lanceolate, some wider than 1 cm, the upper ones distinctly petiolate 18b. subsp. *ovata*

18a. *Lopezia laciniata* subsp. *laciniata*.—FIGS. 92–96.

Stems rigid, \pm erect, short-hirsute. *Leaves* relatively narrow (all narrower than 1 cm), lanceolate or narrowly lanceolate, acuminate at base and apex, the upper ones very short-petioled.

TYPE: Mexico, Jalisco, on mountains near Talpa, 4400–5000 feet elevation, 7 March 1897, *E. W. Nelson 4035* (US; isotype, GH).

Distribution (Fig. 20): Moist seeps in the Sierra Madre Occidental of Jalisco, Mexico, 1400–2000 m elevation. Flowering, October to February.

Additional specimens examined:

MEXICO. JALISCO: Sierra de la Campana 7–8 mi. NW of Los Volcanes, *McVaugh 13760* (BM, MEXU, MICH, RSA, US); Hacienda del Ototal, E of San Sebastián, *Mexia 1688* (BH, BM, G, GH, MO, NY, UC, US); Real Alto to Tranquillas, *Mexia 1714* (BM, DS, MICH, US); NNE of Talpa de Allende, *McVaugh 20347* (MICH).

18b. *Lopezia laciniata* subsp. *ovata* Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 280. 1973.—FIG. 97.

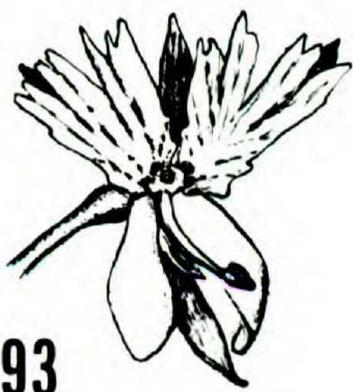
Stems flexible, creeping to ascending, sometimes very slender, subglabrous. *Leaves* ovate to lanceolate, some wider than 1 cm and occasionally to 2.2 cm, subcordate to subacute at base, acute at apex, the upper ones distinctly petioled. Gametic chromosome number, $n = 10$.

Type: Mexico, Durango, 20 mi. W of La Ciudad, steep moist cliff on edge of barranca, 7600 feet, 3 October 1966, *D. E. Breedlove 15552* (DS, holotype).

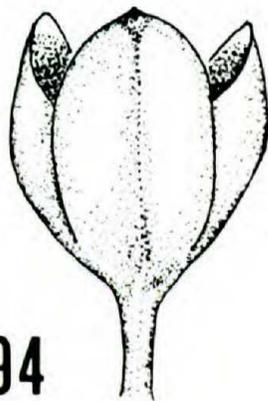
Distribution (Fig. 20): Moist places, usually on wet cliffs and slopes, in rock crevices or near streams, Sierra Madre Occidental of Durango and Sinaloa, Mexico, (800–)1300–2800 m elevation. Flowering, October to February (or March).



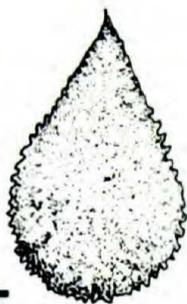
92



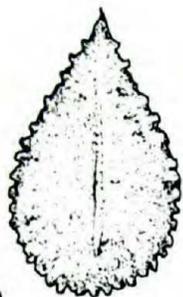
93



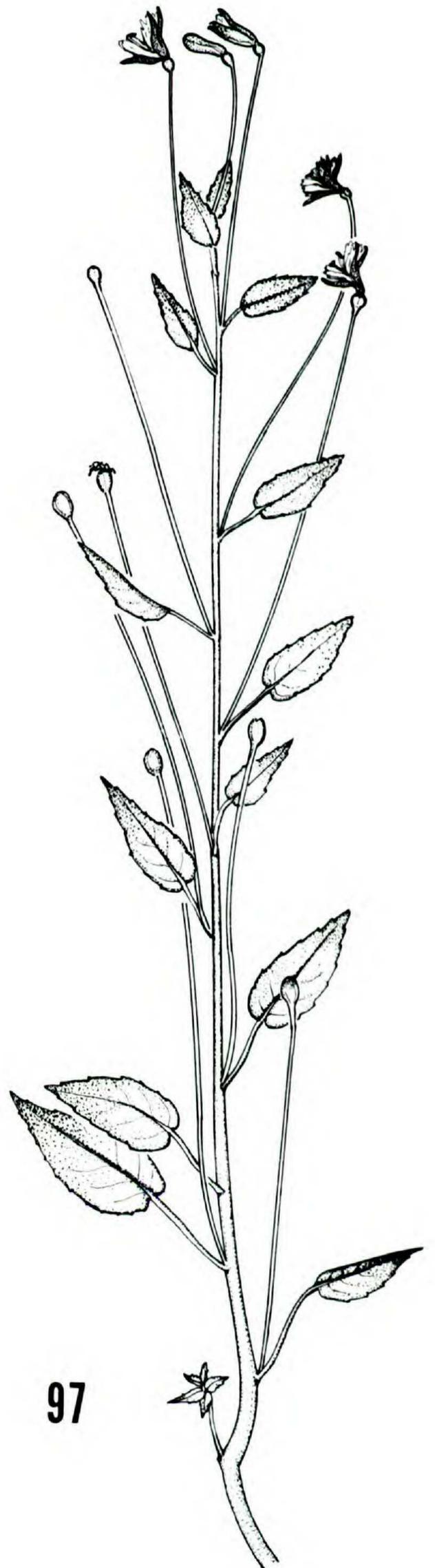
94



95



96



97

Representative specimens examined:

MEXICO. SINALOA: 1 mi. W of El Palmito, ca. 45 mi. E of Concordia, Rosario, *Breedlove* 4248 (DS), *Gentry & Arguelles* 18197 (pedicels up to 5.5 cm; US); 0.4 mi. E of Portrerillos, ca. 34 mi. E of Concordia on Mexican Hwy. 40, Rosario, *Breedlove* 1672 (DS, RSA); Sierra Madre Mts., "El Batel," *Mexia* 468 (MO, UC); El Carrizo, *Ortega* 6035 (POM, US); 59 mi. E of Villa Union, *Wiggins* 13197 (DS). DURANGO: 13 mi. W of La Ciudad, *Breedlove* 15548 (DS), *Flyr* 285 (TEX); 9 mi. E of El Palmito, 55 mi. E of Concordia, Pueblo Nuevo, *Breedlove* 4255 (DS); W slope of Sierra Madre nr El Espinazo, *Ripley & Barneby* 14011 (NY); Los Angeles, Sierra Madre Occidental, *Goodman* 7418 (DS, RSA, UC); 50 mi. WSW of El Santo, *McVaugh* 11589 (MICH).

Particularly in this subspecies, the plants creep and root at the nodes, forming large mats up to several meters across, a habit unique in the genus.

19. *Lopezia gentryi* (Munz) Plitmann, Raven & Breedlove, Ann. Missouri Bot. Gard. 59: 281. 1973.—FIGS. 98–101.

Lopezia laciniata (Rose) Jones subsp. *gentryi* Munz, Brittonia 13: 84. 1961. Munz, N. Amer. Fl. II. 5: 20. 1965.

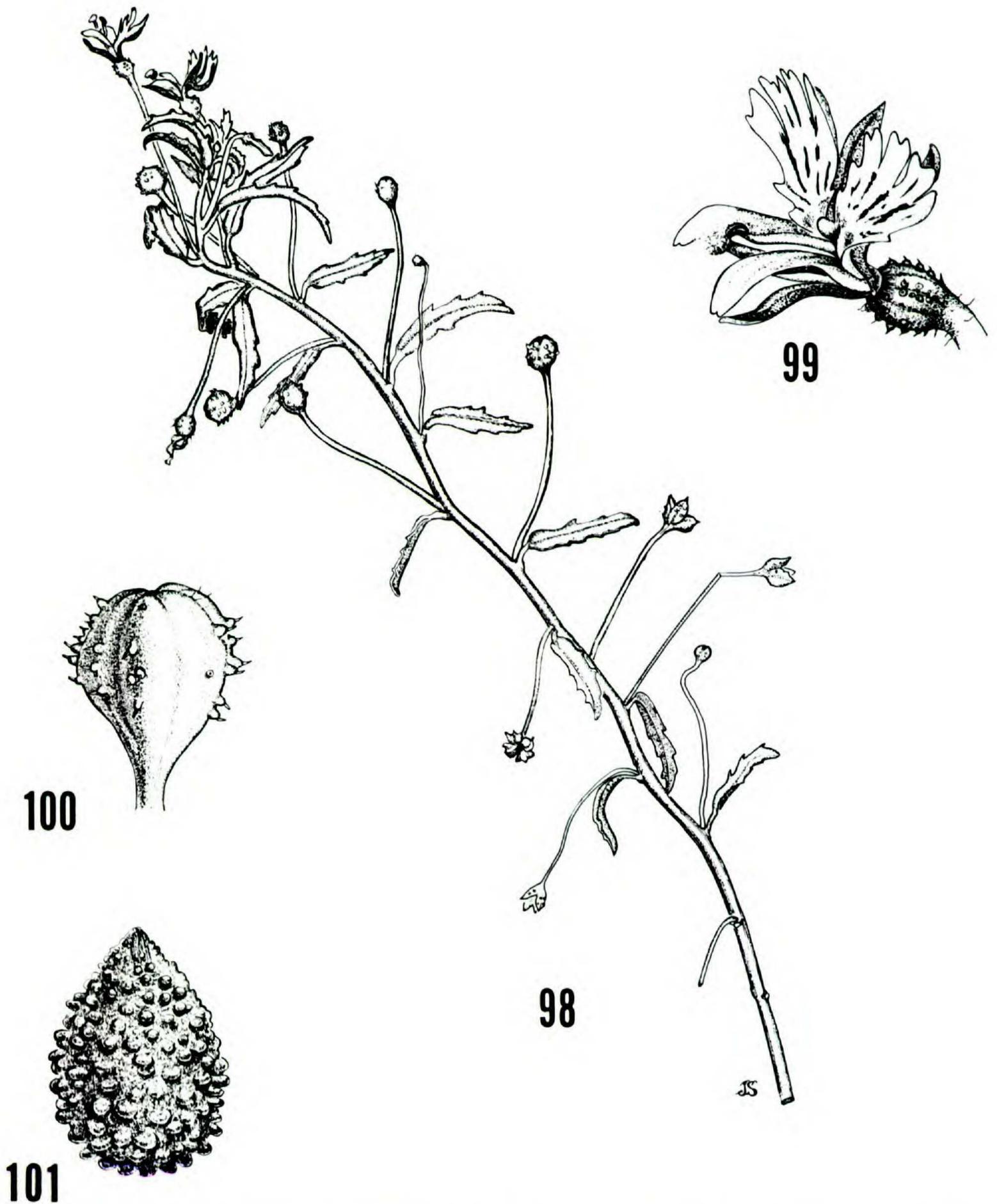
Delicate annual *herbs*, sparsely glandular-puberulent or subglabrous. *Stems* 0.6–2(–2.5) dm tall, thick, slender, decumbent to ascending, sometimes rooting. *Leaves* (0.5–)0.9–2.8 cm long and 0.1–0.7(–1.5) cm wide, narrowly lanceolate or linear, rarely broadly lanceolate, obtuse to angustate at base, \pm acute at apex, serrate or serrulate, green to purplish, subglabrous or very sparsely puberulent; petioles short, 0.1–2.2 cm long, slender, narrowly winged or not, subglabrous. *Bracts* 0.5–1.5 mm wide, rarely wider; pedicels 10–35 mm long, spreading to erect. *Flowers* autogamous. *Sepals* (3–)3.5–4(–5) mm long, ca. 1 mm wide, with a few hairs at the acute apex, often reddish. *Petals* white with red veins; lower petals (2.5–)3.5–5(–6) mm long and 1–1.7 mm wide, linear or lanceolate, subsessile or hardly clawed, entire, subacute or obtuse or somewhat retuse and minutely denticulate at apex; upper petals 3.5–5(–6) mm long and 2.5–3.5 mm wide, obovate, \pm deeply 2–4-lacinate, narrowed at base but not clawed, cleft and dentate or subentire at apex, the margins sparsely dentate. *Fertile stamen* (2.5–)3–4.5(–5) mm long; anther 0.7–1.5 mm long, red. *Pollen* blue. *Staminode* 2–3 mm long, linear, white to sometimes pinkish. *Style* 3–3.5(–4) mm long; stigma 1–1.7 mm in diameter, whitish. *Capsule* 2–3.5 mm long, 1.7–3(–4) mm thick, subglobose (obpyriform), setose toward tip with few or many hairs, these often tuberculate; valves open widely to about a third of their length. *Seeds* ca. 1 mm long, ovoid, somewhat compressed, dark brown to blackish. Gametic chromosome number, $n = 8, 7$.

TYPE: Mexico, Sinaloa, Ocurahui, Sierra Surutato, 6000–7000 feet elevation, 1–10 September 1941, *H. S. Gentry* 6256 (US; isotypes, DS, GH, MO, NY).

Distribution (Fig. 26): Seepages, especially along crevices and ledges, in the Sierra Madre Occidental, Mexico; Sierra Surutato, Sinaloa; along Mexican

←

FIGURES 92–97. *Lopezia laciniata*.—92–96. *L. laciniata* subsp. *laciniata*.—92. Branch, $\times 0.6$.—93. Flower, $\times 3.6$.—94. Capsule, $\times 7.2$.—95. Seed, abaxial view, $\times 24$.—96. Seed, adaxial view, $\times 24$.—97. *Lopezia laciniata* subsp. *ovata*, branch, $\times 1.2$.—Figs. 92–93 from *McVaugh* 13760 (MICH); Figs. 94–96 from *Mexia* 1714 (DS); Fig. 97 from the type collection of subsp. *ovata*.

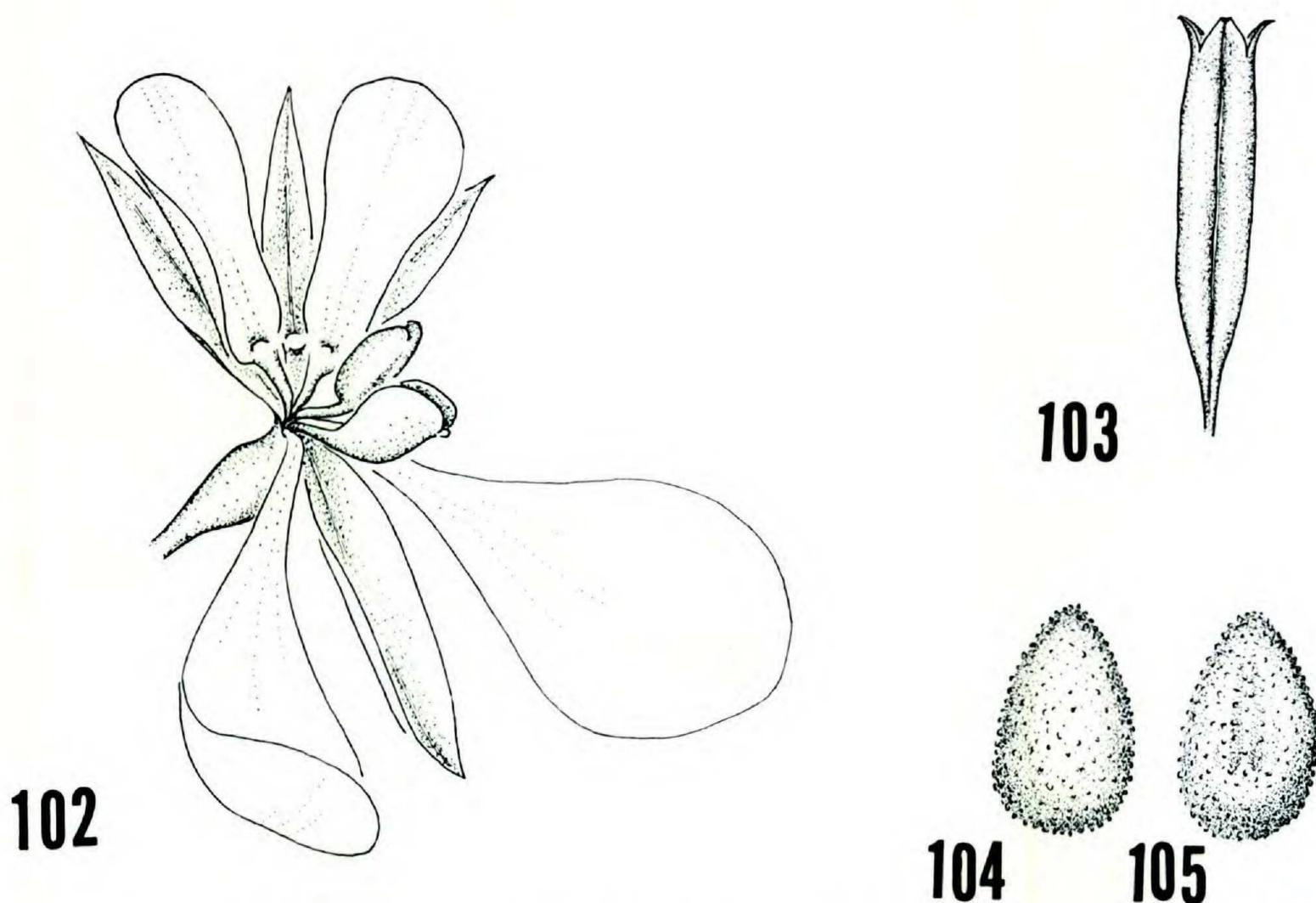


FIGURES 98–101. *Lopezia gentryi*.—98. Inflorescence, $\times 1.3$.—99. Flower, $\times 5.3$.—100. Capsule, $\times 8$.—101. Seed, abaxial view, $\times 26$. All from *Breedlove 15551* (DS).

Highway 40 for about 30 miles, Sinaloa and Durango, 2000–2600 m elevation. Flowering, September and October.

Additional specimens examined:

MEXICO. SINALOA: 3 mi. SE of Los Hornos, Sierra Surutato, *Breedlove & Kawahara 16963* (CAS), *Breedlove & Thorne 18448* (CAS, RSA); 5 mi. NE of La Cienega, Sierra Surutato, *Breedlove & Kawahara 17059* (CAS); 4.4 mi. SW of El Paraíso, Villa Union to El Salto, *Ownbey & Ownbey 1914* (BM, MICH, NY, RSA, UC, US). DURANGO: 17 mi. W of



FIGURES 102–105. *Lopezia clavata*.—102. Flower, $\times 7.4$.—103. Capsule, $\times 4.4$.—104. Seed, abaxial view, $\times 30$.—105. Seed, adaxial view, $\times 30$. All from Moran 7139 (DS).

La Ciudad, *Breedlove 15551* (DS); 20 mi. W of La Ciudad, *Breedlove 1553* (DS); 16 mi. E of El Palmito, *Breedlove 7231* (DS); 5 mi. W of Revolcaderos, 6800 feet, *Breedlove 15555* (DS).

This species is clearly a reduced, annual, autogamous derivative of *Lopezia laciniata* subsp. *ovata*, smaller in all of its parts, and with reduced gametic chromosome numbers of $n = 8$ and 7 instead of $n = 10$.

20. *Lopezia clavata* T. S. Brandege, Proc. Calif. Acad. II, 2: 157, pl. 4. 1889. Munz, Brittonia 13: 82. 1961; N. Amer. Fl. II. 5: 19. 1965.—FIGS. 102–105.

Pelozia clavata (Brandege) Rose, Contr. U. S. Natl. Herb. 12: 296, fig. 37. 1909.

Glandular-puberulent and sparsely pilose to glabrous annual herbs. Stems 2–6.5 dm tall, erect; branches glabrous to \pm densely pilose with patent short and long hairs. Leaves thin, sparsely and \pm divaricately pilose or puberulent to glabrous; lower leaves 1.5–8 cm long and 0.7–6 cm wide, ovate to lanceolate, rounded or broadly cuneate and sometimes asymmetrical at base, acute or acuminate at apex, serrate or serrulate, sometimes ciliolate, with 5–10 veins on each side of midrib; upper leaves 0.25–0.7 cm wide, lanceolate, obtuse at base, angustate at apex, subserrate or serrulate; petioles 0.15–3.5 cm long and ca. 0.1 cm wide, slender, patent-pilose to subglabrous, some narrowly winged. Inflorescences \pm pilose to subglabrous; bracts 3–25 mm long, 1–9 mm wide, glabrous; pedicels 5–27(–35) mm long, ascending to erect, \pm pilose to subglabrous. Flowers mostly autogamous. Sepals 3.5–6 mm long, subglabrous.

Petals pinkish or lilac to sometimes red or purplish; lower petals (3–)5–9 mm long and 2–4.5 mm wide, obovate, clawed-angustate at base, rounded at apex; upper petals (2.5–)4–6 mm long and 0.7–2.5 mm wide, oblong-spatulate, slightly dilate then somewhat clawed at base, obtuse at apex. *Fertile stamen* 1.5–3 mm long; anther 1.5–1.7 mm long, yellowish. *Pollen* yellow. *Staminode* 2–3 mm long and 1–2 mm wide, obovate-spatulate, clawed, retuse at apex, white or reddish. *Style* ca. 2 mm long; stigma 0.5–0.8 cm in diameter, lilac; ovary 1.5 mm long, 0.5–1 mm thick, ellipsoid, \pm pilose near tip. *Capsule* (4–)5–10(–13) mm long, 1.2–2.5 mm thick, clavate-obconical or subcylindrical, tapering at base, truncate and dentate at tip, pilose with apical hairs to subglabrous, erect; valves open at summit only as erect or divaricate teeth. *Seeds* 0.5–1 mm long, oblong or ovoid, brown. Gametic chromosome number, $n = 9$.

TYPE: Mexico, Baja California, Comondú Cañon, base of cliffs, 19 February 1889, T. S. Brandegees (UC; isotypes, GH, US).

Distribution (Fig. 34): Near streams or in moist or shaded places, usually on sandy soil, in Baja California Sur, Mexico, from the Sierra de la Giganta to the mountains of the Cape region, and on Isla Partida in the Golfo de California, 100–1800 m elevation. Flowering, October to March.

Representative specimens examined:

MEXICO. BAJA CALIFORNIA: Cape Region Mts., Brandegees, 1899 (POM), 1902 (GH, UC, US), Erabendorffer, 1891 (UC), Moran 7139 (DS, IPN), 7090 (DS, IPN), Thomas 7850 (DS, RSA); Saucito, Brandegees, 1893 (UC); Sierra de Laguna, Brandegees 221 (UC), Nelson & Goldman 7433 (POM, US), Hammerly 367 (DS, GH, US), Carter et al. 2392a (DS, GH, MO, S, US), 2392 (DS, GH, US); Arroyo Hondo, Sierra Giganta, Gentry 4123 (DS, GH, MO, UC, US), Carter et al. 2019 (DS, US); Arroyo Quisapol, E of La Presa, Sierra de la Giganta, Wiggins 15542 (DS); La Campana, Sierra de las Palmas, Gentry & Fox 11791 (MEXU); Arroyo de San Bartolo, Wiggins 14752 (DS, IPN, MEXU, TEX, UC); Arroyo de León, 22 mi. SE of La Paz to Las Planes, Wiggins et al. 472 (DS, MEXU, UC), Porter 248 (DS, MEXU); San Bartolo, Jones 24287 (POM); W shore of Isla Partida, Wiggins et al. 405 (DS, MEXU, UC); Laguna Mts., Jones 24153 (DS, MICH, MO, NY, POM, UC, US), 24288 (MICH, MO, NY, POM, UC, US); Todos Santos, Jones 24286 (POM, US); El Taste ridge, NE of La Carrerita, Carter & Chisaki 3531, 3574 (both RSA); San José del Cabo, Jones, 1928 (POM); S of Miraflores, Wiggins 14734 (DS); E slope of Cerro Barranco, Sierra Santa Lucia, Moran 11786 (DS); Arroyo San Martes, 6 mi. SW of Santiago, Thomas 7721 (DS).

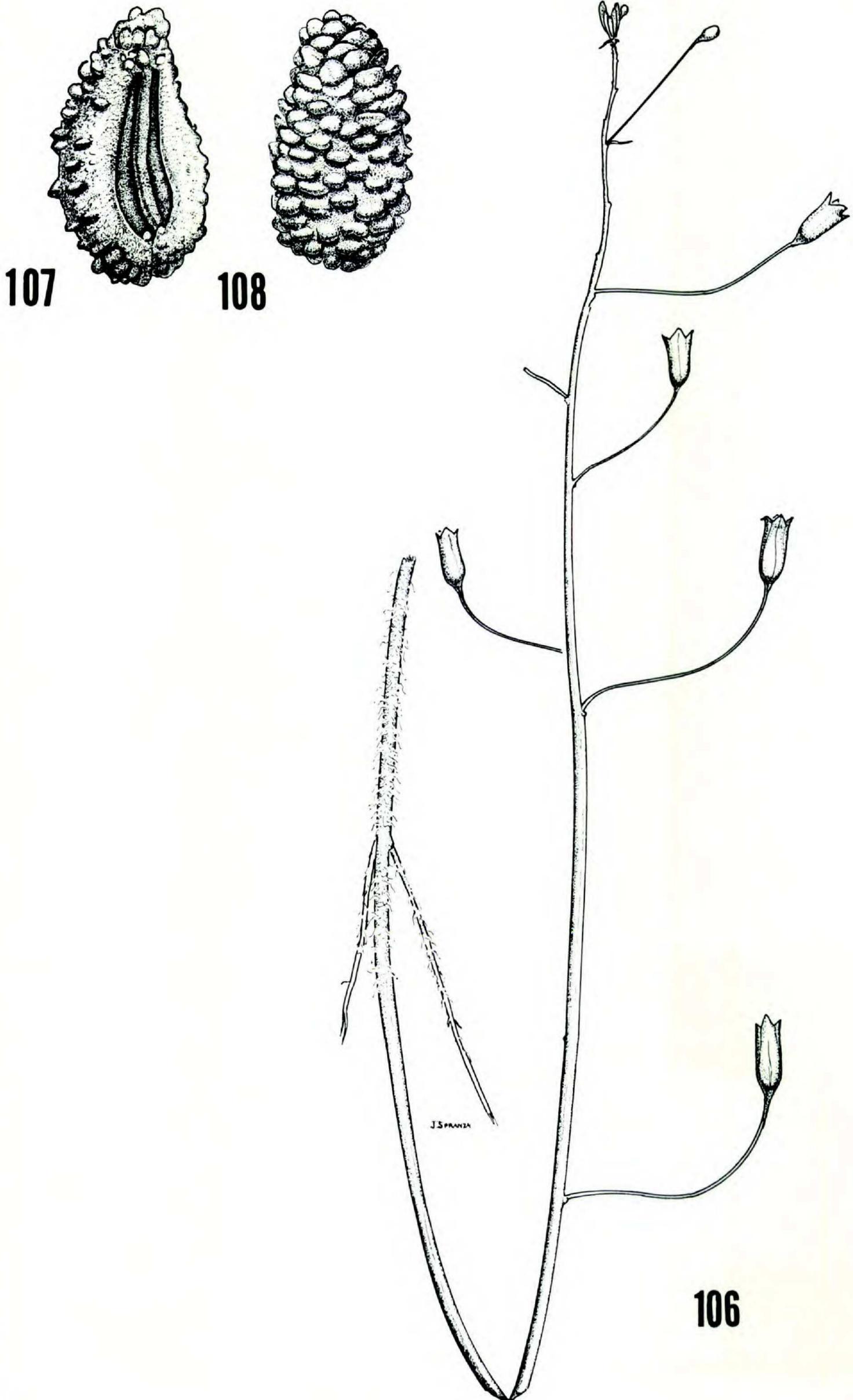
This species is extremely variable in the size and hue of its flowers and in the dimensions of its leaves and capsules.

21. *Lopezia sinaloensis* Munz, Brittonia 13: 83. 1961. Munz, N. Amer. Fl. II. 5: 20. 1965.—FIGS. 106–108.

Densely pilose with patent or retrorse long hairs. *Stems* ca. 3 dm tall. *Leaves* ca. 1–2.5 cm long (or longer?), ovate, obtuse or acute, subentire, the upper smaller, linear; petioles ca. 0.3–1.2 cm long. *Inflorescence* few-flowered. *Pedicels* ca. 20–25 mm long, slender, sigmoid-spreading in fruit. *Flowers* much as in *L. clavata*. *Sepals* ca. 5 mm long. *Petals* pale pink, the lower ones ca. 7 mm long,

→

FIGURES 106–108. *Lopezia sinaloensis*.—106. Branch, \times 1.2.—107. Seed, adaxial view, \times 25.—108. Seed, abaxial view, \times 25. All from the holotype.



107

108

106

narrowly obovate, long-clawed; the upper ones ca. 5 mm long, lanceolate, scarcely clawed, eglandular. *Fertile stamen* not known. *Staminode* ca. 5 mm long, angustate at base, obcordate at apex, white. *Style* ca. 2 mm long. *Capsule* ca. 8 mm long, ca. 3 mm thick, cylindrical-clavate, open at summit only. *Seeds* ca. 1 mm long, transversely tubercled and suberoded, black.

TYPE: Mexico, Sinaloa, Cuesta (or Cueva or Curva) del Diablo, Municipalidad Concordia, September 1919, *M. P. Dehesa 1561* (US).

Distribution (Fig. 34): Mexico, endemic in central Sinaloa, at lower elevations; apparently rare, and apparently known only from one gathering.

Specimen examined:

MEXICO. SINALOA: Concordia, Mazatlán, *Ortega 1561* (MEXU, number of type collection).

A rare species of which the type is the only known collection. Munz (1961) distinguished it from *Lopezia clavata* mainly by its larger flowers. In view of the wide variability of the latter, this distinction is unsatisfactory. More relevant dissimilarities are found in the pilosity of stems, morphology of upper petals, length of staminode, thickness of capsules, surface of seeds and to some extent also in leaf-margins and in the color of sepals and petals. The two species are very similar and further material of *L. sinaloensis* will be necessary before they can be compared adequately.

DOUBTFUL NAMES AND EXCLUDED SPECIES

Lopezia bracteata Rafin., *Autikon Botanikon* 13. 1840.—Description inadequate, authentic material unknown. Said to be from New Mexico; doubtfully *Lopezia*.

L. glazioui H. Leveille, *Fedde Repert. Nov. Sp.* 4: 226. 1907 = *Diplusodon virgatus* Pohl (Lythraceae).

LITERATURE CITED

- AITON, W. 1810. *Hortus Kewensis; or, a Catalogue of the Plants Cultivated in the Royal Botanic Garden at Kew.* Ed. 2. London.
- BAEHNI, C. & C. E. B. BONNER. 1948. La vascularisation des fleurs chez les *Lopezieae* (Onagraceae). *Candollea* 11: 305–322.
- BAILLON, H. 1877. LVIII. Onagrariacées. *Histoire des Plantes* 6: 458–499. Paris.
- BENTHAM, G. & J. D. HOOKER. 1862. *Genera Plantarum.* Vol. 1. London.
- BRANDEGEE, T. S. 1889. A collection of plants from Baja California, 1889. *Proc. Calif. Acad. Sci.* II. 2: 117–216.
- DE CANDOLLE, A. P. 1828. *Prodromus Systematis Naturalis Regni Vegetabilis.* Vol. 3. Paris.
- DE VRIES, H. 1894. Over de Erfelijkheid van Fasciatien. *Bot. Jaarb. Dodonaea* 6: 72.
- . 1899. Sur la culture des fasciations des espèces annuelles et bisannuelles. *Rev. Gén. Bot.* 2: 136–151.
- ENDLICHER, S. L. 1840. *Genera Plantarum secundum Ordines Naturales Disposita.* Vienna.
- . 1841. *Enchiridion Botanicum exhibens Classes et Ordines Plantarum, accedit nomenclator generum ex officinalium vel usualium indicatio.* Leipzig and Vienna.
- EYDE, R. H. & J. T. MORGAN. 1973. Floral structure and evolution in *Lopezieae* (Onagraceae). *Amer. Jour. Bot.* 60: 123–456.
- FISHER, F. J. F. 1965. The alpine *Ranunculi* of New Zealand. *New Zealand Dept. Sci. Indust. Res. Bull.* 165: 1–192.
- FOSTER, R. C. 1945. The rediscovery of *Riesenbachia* Presl. *Contr. Gray Herb.* 155: 60–62.
- GATES, R. R. 1910. Abnormalities in *Oenothera*. *Missouri Bot. Gard. 21st Ann. Rep.* 175–184.
- JOHANSEN, D. A. 1930. Studies on the morphology of the Onagraceae. II. Embryonal manifestations of fasciation in *Clarkia elegans*. *Bot. Gaz.* 90: 75–91.

- JONES, M. E. 1929. Notes and new species of Mexican plants. *Contr. West. Bot.* 15: 123-157.
- KNOX, A. A. 1907. The relation of injury to fasciation in the evening primrose. *Pl. World* 10: 145-151.
- . 1908. Induction, development and heritability of fasciations. *Carnegie Inst. Publ.* 98: 1-21.
- KRUTZSCH, W. 1968. Zur Kenntnis des Dispersen Oenotheraceen-(Onagraceen-) Pollens, insbesondere aus dem mitteleuropäischen Tertiär. *Paläontol. Abh., Abt. B* 2: 765-788; *Taf. 1-5*.
- KURABAYASHI, M., H. LEWIS & P. H. RAVEN. 1962. A comparative study of mitosis in the Onagraceae. *Amer. Jour. Bot.* 49: 1003-1026.
- LEWIS, H. 1962. Catastrophic selection as a factor in speciation. *Evolution* 16: 257-271.
- . 1973. The origin of diploid neospecies in *Clarkia*. *Amer. Naturalist* 107: 161-170.
- & M. E. LEWIS. 1955. The genus *Clarkia*. *Univ. Calif. Publ. Bot.* 20: 241-392.
- & M. R. ROBERTS. 1956. The origin of *Clarkia lingulata*. *Evolution* 10: 126-138.
- MALFAIT, B. T. & M. G. DINKELMAN. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. *Geol. Soc. Amer. Bull.* 83: 251-272.
- MCVAUGH, R. 1956. Edward Palmer. Plant Explorer of the American West. Univ. of Oklahoma Press, Norman.
- MIRANDA, F. 1953. Plantas nuevas o notables de la flora de Chiapas. *Anal. Inst. Biol. Méx.* 24: 69-96.
- . 1962. *Lopezia langmanae* and the genus *Jehlia*. *Brittonia* 14: 46-47.
- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev.* 45: 417-450.
- MUNZ, P. A. 1961. The Lopezieae (Onagraceae). *Brittonia* 13: 73-90.
- PLITMANN, U., P. H. RAVEN & W. TAI. 1974. Cytological studies in Lopezieae (Onagraceae). In preparation.
- RAIMANN, R. 1893. Onagraceae. In A. Engler & K. Prantl, "Die Natürlichen Pflanzenfamilien." III(7): 199-223.
- RAVEN, P. H. 1964. The generic subdivision of Onagraceae, tribe Onagreae. *Brittonia* 16: 276-288.
- , D. E. BREEDLOVE, D. P. GREGORY & U. PLITMANN. 1974. The floral biology of Lopezieae (Onagraceae). In preparation.
- RILEY, L. A. M. 1924. Contributions to the flora of Sinaloa: V. *Kew Bull.* 1924: 206-222.
- ROSE, J. N. 1909. Studies of Mexican and Central American plants. No. 6. *Contr. U. S. Natl. Herb.* 12: 259-302, *pl. 20-27* [Lopezieae, pp. 294-301].
- SCHUCHERT, C. 1935. Historical geology of the Antillean-Caribbean region. John Wiley & Sons, New York.
- SPACH, E. 1835. Onagraires. *Hist. Nat. Vég.* 4: 335-416.
- SPRAGUE, T. A. & L. A. M. RILEY. 1924. A recension of *Lopezia*. *Jour. Bot. Brit. Foreign* 62: 7-16.
- STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.
- STEIN, F. 1915. Über Ölkörper bei Oenotheraceen. *Öst. Bot. Zeit.* 65: 43-49.
- WATSON, S. 1886. Contributions to American botany. [XIII.] *Proc. Amer. Acad. Arts* 21: 414-468.
- WILLIS, J. C. 1966. A Dictionary of the Flowering Plants and Ferns. Seventh Ed., revised by H. K. Airy Shaw. Cambridge Univ. Press, Cambridge.